UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1429

Washington, D. C. ▼ January, 1927

THE PARASITES OF POPILLIA JAPONICA IN JAPAN AND CHOSEN (KOREA), AND THEIR INTRODUCTION INTO THE UNITED STATES

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THE GENERAL PROBLEM

The foreign work [2] in regard to the natural enemies of the so-called Japanese beetle (*Popillia japonica* Newm.) represents one phase of the general problem dealing with the control of this rapidly increasing insect. The work in Japan was initiated in the early spring of 1920, with headquarters at Yokohama, and investigations have been in progress continuously since that time, being confined for the first two years to Japan and extended in 1922 to Chosen. It is expected that importations of the various parasites found will be continued until establishment is certain, or it is demonstrated that environmental and other factors do not permit of its accomplishment.

[1] Valuable assistance was rendered in this work by Kaku Sato, who has been engaged on the project for the last three years. Yoshiro Ouchi also joined the force in 1923.

[2] During the writers' sojourn in Japan they were most courteously received and aided by all the Japanese Government departments, particularly by the department of agriculture and commerce. Special appreciation is felt for the great help rendered in many ways by S. I. Kuwana, director of the imperial plant quarantine station, and his staff. Thanks are also due to S. Matsumura, professor of entomology at the Hokkaido Imperial University, for the use of the university collections; to H. Okamoto, entomologist of the Government general agricultural experiment station at Suigen, Chosen; to S. Kuwayama, entomologist of the Hokkaido Agricultural Experiment Station; and to the directors of the two last named stations, where laboratory facilities were kindly provided during the course of the field work.

To Baron Iwasaki and the directors of his estate at Koiwai grateful acknowledgements are made for working quarters during three seasons and for privileges which permitted an extended investigation of the most important area, from the point of view of Popillia parasites, thus far found in Japan.

Determination of species and descriptions of those which proved to be new have been made by J. M. Aldrich of the United States National Museum and S. A. Rohwer of the Bureau of Entomology, the former dealing with the Diptera and the latter with the Hymenoptera.

Popillia japonica was first found in the United States near Riverton, N. J., in the summer of 1916. The beetles no doubt entered this country in soil surrounding the roots of Japanese nursery stock shipped into Burlington County, N. J., at a date shortly prior to 1916. When first found the infestation covered an area of approximately one-half square mile and the beetles were exceedingly scarce, only about a score having been taken at that time. The increase in the area infested has been so great that the pest now (1925) covers some 6,047 square miles. The beetle is an omnivorous feeder and in recent years has caused serious destruction to both cultivated and native plants within this area, and to fruit and shade trees.

In the central portion of the infested area the numerical increase has been incredible, as is shown by the following statement from a recent publication by L. B. Smith, in charge of the Japanese beetle laboratory at Riverton:

> During July, 1923, in an orchard of one hundred fifty-six 10-year-old Redbird peach trees, thirteen 16-gallon tubfuls of beetles were shaken from the trees and collected early one morning, in somewhat less than two hours. The next morning the beetles were apparently as numerous on these trees as before. [3]

Popillia japonica entered the United States apparently free from its natural enemies, and its increase has been due not only to this fact, but to an acceleration of development in a new and apparently ideal environment. Under these circumstances it has become one of the major insect pests of the sections in which it now occurs. American parasites and predators thus far seem to be a negligible factor in preying upon it, and mechanical and cultural control methods are so far not wholly effective. In view of these facts the necessity for an attempt at control by the biological method is evident.

THE FIELD OF INVESTIGATION

The investigations in Japan were begun in 1920 at Nagasaki in the south (fig. 1) and extended northward as the season advanced. On account of existing agricultural conditions and methods in the southern half of the country and the absence of waste land, it was almost impossible to conduct extensive scouting for grubs in the soil. During the first 10 weeks of search only 76 grubs of *Popillia japonica* were found, even though beetles were later fairly common. With so small a number of grubs available, it was evident that the chance of finding parasites upon them would be very slight. and that extensive experimental tests with the various Scoliidae and other parasitic species collected as adults in the field would be impossible. It was only on the arrival of the writers at Koiwai, in northern Japan, on July 12 that beetles and grubs were found in sufficient numbers to give hope of success in the search for parasites. It was in these northern sections that the greater number of parasite species were eventually obtained.

Although *Popillia japonica* itself was not found in Chosen, the presence of other species of the same genus gave promise of additional parasites of value. The five species of the latter found there substantiated this conclusion, since it was determined that none of these species was specific in its choice of hosts, but would reproduce equally well upon *P. japonica*.

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[3] Smith, L. B. Service and Regulatory Announcements, Federal Horticultural Board, U. S. Department of Agriculture, October–December, 1923, p. 150.

In July of 1923 a scouting trip was undertaken through the central portions of Manchuria, extending from Antung on the Chosen border to Harbin in the north. The greater part of this area is very flat and almost entirely devoid of trees and shrubs. Only two species of Popillia (*P. castanoptera* Hope and *P. mutans* Newm.) were found in

FIG. 1.—Map of Japan and Chosen (Korea) showing the main areas in which *Popillia japonica* and its parasites were studied

this section, and in such very small numbers as not to admit of parasite investigations.

THE PARASITES AND THEIR BIOLOGY

In the course of the investigations nine parasites of *Popillia japonica* and related species were found and their relations to the host species determined. In addition, one predator was studied in some

detail, and extensive shipments were made. The complete list is here given, those starred being found under natural conditions parasitic upon *P. japonica* itself.

Parasites of the adult beetle:
- **Centeter cinerea* Aldrich (Diptera, Tachinidae).
- **Eutrixopsis javana* Townsend (Diptera, Tachinidae).
- **Ochromeigenia ormioides* Townsend (Diptera, Tachinidae).

Parasites of the larva:
- **Prosena siberita* (Fabricius) (Diptera, Dexiidae).
- *Dexia ventralis* Aldrich (Diptera, Dexiidae).
- *Campsomeris annulata* (Fabricius) (Hymenoptera, Scoliidae).
- **Tiphia popilliavora* Rohwer (Hymenoptera, Scoliidae).
- *Tiphia vernalis* Rohwer (Hymenoptera, Scoliidae).
- *Tiphia koreana* Rohwer (Hymenoptera, Scoliidae).

Predator:
- *Craspedonotus tibialis* Schaum (Coleoptera, Carabidae).

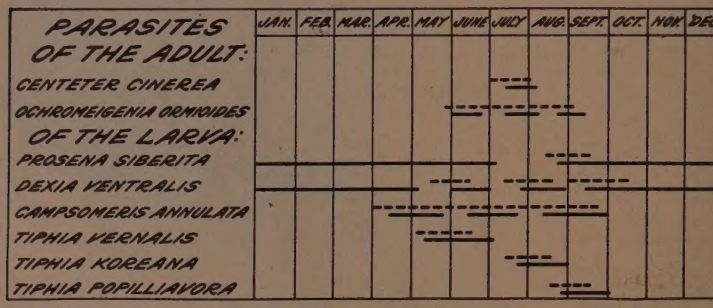

FIG. 2.—The sequence of parasites of *Popillia japonica* and related species. The dotted line represents the period during which adults may be found in the field, and the solid line indicates the time during which living parasitized hosts may be found

In Figure 2 is given a representation of almost the entire series of parasites as regards their time of appearance and the stage of the host attacked. It is seen that all the species with the exception of the two dexiids pass the winter in the puparium or cocoon stage, these two species carrying over as early-stage larvæ within the host grubs.

In a consideration of this chart, it must be borne in mind that the periods given are as they occur under Japanese or Chosen conditions, which in some cases differ greatly from those in the infested area in America, and certain of the parasites are upon host species which have a different life cycle from that of *Popillia japonica* in the latter locality. The bearing of these factors upon the possible usefulness of the species in America will be discussed in detail in the account of the individual species.

CENTETER CINEREA Aldrich [4]

The first evidence of parasitism of adult *Popillia japonica* by *Centeter cinerea* (fig. 3) was secured by the senior author on July 12, 1920, at Koiwai, Iwate-ken, about 300 miles north of Tokyo. Here the beetles were found abundantly feeding upon the foliage of itadori (*Polygonum reynoutria*) (fig. 4) and other weeds, and a considerable proportion of them bore tachinid eggs upon the thorax.

[4] Determined by Doctor Aldrich as a new genus and species, and described under the above name. Aldrich, J. M. Two Asiatic muscoid flies parasitic upon the so-called Japanese beetle. Proc. U. S. Natl. Mus., Vol. 63, pp. 1–4. 1923.

The number of eggs present indicated that the attack was more than incidental. Observations were extended to the various sections north of Koiwai and to Hokkaido, the northern island. Here, at Sapporo, the proportion of beetles bearing these tachinid eggs approached 100 per cent. It was evident that this was a parasite capable of exerting a marked check upon *Popillia japonica*, and that it might well be of equal value if introduced into America.

FIG. 3.—*Centeter cinerea*, female

Arrangements were at once made to study the species both at Koiwai and at Sapporo, to determine its life history, its method of parasitism, and other points in its biology which might prove of value in determining its relation to the host. Ways and means of breeding and handling were also sought in order that its importation into the United States in the living condition might be assured. These studies were continued for some 10 days, and a small number of parasitized beetles collected and confined in cages for observation, when the sudden and unexpected disappearance of both the host and parasite at Sapporo, and of the latter only at Koiwai,

FIG. 4.—Clumps of itadori (*Polygonum reynoutria*), a favorite food plant of *Popillia japonica*, Koiwai, Japan

interrupted the work for the season. This was a development which was entirely unexpected, since the beetle itself had been present in numbers for not more than two weeks and it was

presumed that the activities of the parasite would be extended over a greater period of time.

No further studies upon the species being possible that season, attention was turned to the finding of other natural enemies of *Popillia japonica*. Observations were renewed in 1921, and in that and the following year studies and collections were made both at Koiwai and at Sapporo immediately upon the appearance of the first beetles of the season. In 1923 final observations and collections were made at Sapporo only, since at this place conditions for the work were nearly ideal, the area infested by the beetle being of considerable extent, the parasites abundant, and collectors available in unlimited numbers (fig. 5). Although the parasite is usually found in most localities north of Morioka, the greater part of the work was conducted at Sapporo because of the favorable conditions prevailing there.

FIG. 5.—Children engaged in collecting Popillia beetles parasitized by *Centeter cinerea*, Sapporo, Japan

As is pointed out in the account of the life history of *Popillia japonica* in Japan, there is for the most part a pronounced two-year life cycle in Hokkaido, resulting in an abundance of beetles every second year (1921 and 1923), with a lesser number during the alternate years. At Koiwai, although some of the grubs carry over for two years, the number of beetles emerging each year is fairly constant. This point is elaborated in the discussion of the life history of the host. Such deviation from the normal one-year cycle has had a pronounced influence upon the parasite itself as will be shown later.

FIELD OBSERVATIONS

Centeter cinerea was under close observation during the years 1920 to 1923, inclusive, and its behavior over this period has given a fair indication of its possibilities. Figure 6 shows the relative abundance of the beetle at Sapporo during the period mentioned, and the percentage of parasitism effected by *C. cinerea*. In 1920 the beetles were relatively scarce; the parasitism of the females exceeded 90

per cent during the time immediately following emergence, resulting in an abrupt reduction in numbers and the complete disappearance of the beetles by about the end of July, much earlier than would normally have been the case.

In 1921 this state of affairs was somewhat reversed, the beetles being approximately three times as abundant as in the previous year, whereas at no time did more than 31 per cent of the females bear eggs. The 1922 season practically duplicated that of 1920 in beetle scarcity and parasite abundance, whereas in 1923 the conditions of 1921 were repeated. The numerical abundance of *Centeter cinerea* is therefore in an inverse ratio to that of the host, the parasite being abundant when the host is at its lowest point, and vice versa. In the years of beetle scarcity there is a great duplication of oviposi-

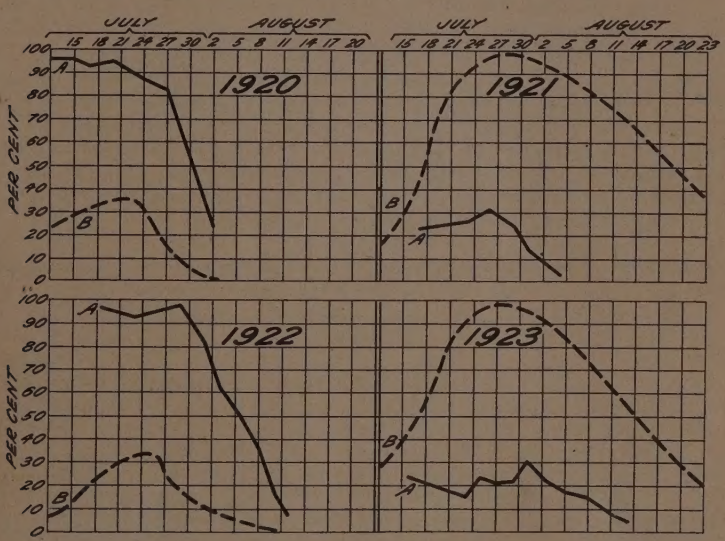

FIG. 6.—Curves showing the biennial broods of *Popillia japonica* at Sapporo, Japan, for 1920 to 1923, inclusive, and the relative parasitism of the female beetles by *Centeter cinerea*: A, percentage of beetles parasitized by *C. cinerea*; B, seasonal curve for abundance of adults of *P. japonica*, that for 1921 and 1923 being considered as approximately 100 per cent

tion by the parasite, female beetles having been found bearing as many as 14 eggs upon the body, whereas the average for 1,135 parasitized females was 4 eggs. Inasmuch as only one individual normally develops in a single host, it is evident that at this point a considerable proportion of the potential rate of increase is lost. The final result is that the following year sees a reduction in the actual number of flies available to parasitize the much greater number of beetles. In consequence, very little oviposition duplication occurs, as is shown by the fact that of 401 beetles bearing eggs, the average number of eggs borne was 1.1 per parasitized female. As a direct result of this a much greater proportion attain maturity than in the preceding generation, and thus the biennial cycle once more begins.

It may be well to consider the data obtained by counts made in the field during the years 1921 to 1923, inclusive, at Sapporo and Koiwai.

This is given in Table 1. At Koiwai the beetles were present in about equal numbers each year, and consequently conditions in this respect more nearly approach those found in New Jersey and Pennsylvania. Few actual counts were made in 1920, and none in 1923, so that data for only two years are available. It is known, however, that the general parasitism in 1920 approximated that of the following two years. It may be explained that in taking these data mating pairs were collected in the field and the number of eggs borne by each sex recorded. In this way a representative series of each sex was secured, and the figures are felt to be a fairly accurate representation of field conditions at the time the observations were made. The general averages cover the period from the appearance of the beetles in numbers to the cessation of oviposition by the parasite.

Reference to the tabulated data for Koiwai shows that in 1921 (Table 1) 42.1 per cent of the female beetles observed bore *Centeter cinerea* eggs, with an average of 1.4 per parasitized female. The males, on the contrary, were attacked only to the extent of 1.1 per cent. Of all eggs, 95.9 per cent were deposited upon female beetles. An explanation of this will be given later in the discussion of the manner of oviposition of the parasite. During 1922 the parasitism was somewhat higher than in the preceding year, the percentage being 58.4 for the females and 16.2 for the males, and the proportion of the egg total on the former 85.9 per cent.

TABLE 1.—*Field parasitism by Centeter cinerea at Sapporo and Koiwai, Japan, 1921–1923*

	Sapporo				Koiwai			
	Females		Males		Females		Males	
1921								
Total number of beetles examined	812	*Per cent*	812	*Per cent*	1,584	*Per cent*	1,985	*Per cent*
Total number bearing *C. cinerea* eggs	158	19.5	32	3.9	667	42.1	36	1.8
Total number of eggs present	190		32		934		40	
Proportion on each sex		85.6		14.4		95.9		4.1
Maximum parasitism		22.6		4.7		53.2		6.3
Maximum number of eggs on one beetle	4		1		5		2	
Average per parasitized beetle	1.2		1.0		1.4		1.1	
1922								
Total number of beetles examined	1,292		1,292		500		500	
Total number bearing *C. cinerea* eggs	1,135	87.8	670	51.9	292	58.4	81	16.2
Total number of eggs present	4,507		1,096		614		101	
Proportion on each sex		80.4		19.6		85.9		14.1
Maximum parasitism		100.0		84.3		62.0		25.0
Maximum number of eggs on one beetle	14		6		6		2	
Average per parasitized beetle	4.0		1.6		2.1		1.2	
1923								
Total number of beetles examined	2,122		2,071					
Total number bearing *C. cinerea* eggs	401	18.9	22	1.1				
Total number of eggs present	475		22					
Proportion on each sex		95.6		4.4				
Maximum parasitism		30.5		1.5				
Maximum number of eggs on one beetle	4		1					
Average per parasitized beetle	1.2		1.0					

At Sapporo, with its biennial periodicity in beetle abundance, in 1921 there was an average parasitism in the females of 19.5 per cent, of the males 3.9 per cent, with 85.6 per cent of the egg total on female beetles. The following year revealed a parasitism of female beetles to the extent of 87.8 per cent, of the males 51.9 per cent, and the proportion of eggs on female beetles was 80.4 per cent. The third year, 1923, revealed 18.9 per cent of female beetles bearing parasite eggs, 1.1 per cent of the males, and 95.6 per cent of the egg total on the former. It is thus seen that conditions in 1921 and 1923 were practically identical and, though lacking exact figures for 1920, it is known that the parasitism for that year was approximately equal to that for 1922. These four years may therefore be taken as illustrating the normal cycle of *Centeter cinerea* at Sapporo.

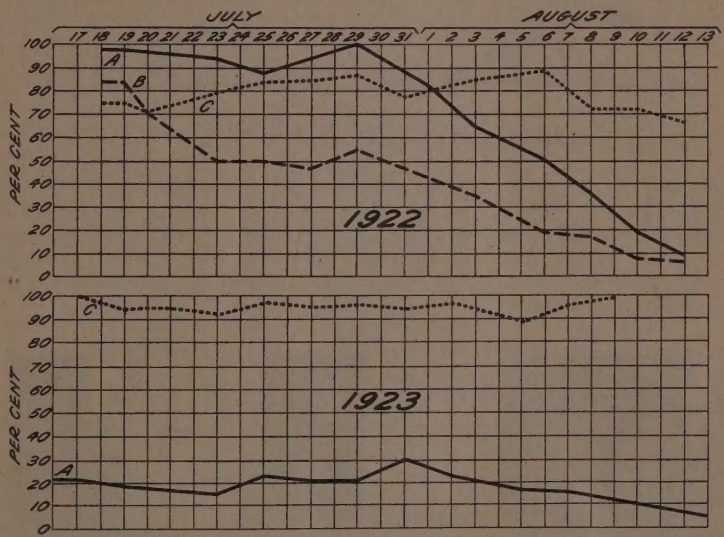

FIG. 7.—Curves showing the percentage of parasitism of *Popillia japonica* by *Centeter cinerea* at Sapporo, Japan, in 1922 and 1923: A, parasitism of female beetles; B, parasitism of male beetles; C, proportion of eggs laid upon female beetles

In Figures 7 and 8 are given in graphic form the data on parasitism at Sapporo in 1922 and 1923, and for 1921 at Koiwai, these being the years when most extensive data at these places were obtained. The most striking difference in the graphs for Sapporo is that for the parasitism of the males, which in 1923 never exceeded 1.5 per cent, and therefore was too low to be represented on the chart, in 1922 attained a maximum of 84.3 per cent. In both years the graphs representing the proportion of eggs on female beetles remained approximately constant throughout the season, as it did also at Koiwai.

The full effectiveness of this parasite is not indicated by the figures previously given, but is in reality somewhat greater. Life-history studies have shown that the beetles are killed within a period of six days after the parasite eggs are deposited; consequently practically all beetles bearing eggs on any given date are dead within six days thereafter, and the parasitized beetles in the field at the latter date

represent an additional percentage of the total. To illustrate this point, the graph representing the parasitism of female beetles at Koiwai during 1921 (fig. 8) may be cited. On July 14, 35 per cent bore eggs, these being replaced on the 20th by 45 per cent of the remainder, the latter in turn being replaced by 48.5 per cent of those

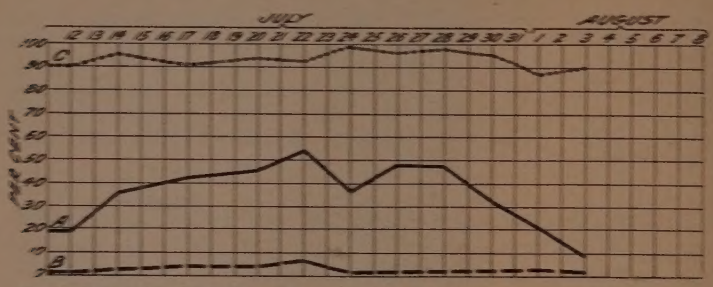

FIG. 8.—Curves showing the percentage of parasitism of *Popillia japonica* by *Centeter cinerea* at Koiwai, Japan, during 1921: A, parasitism of female beetles; B, parasitism of male beetles; C, proportion of eggs laid upon female beetles

remaining on the 26th. Thus, theoretically, the parasitism effected was 35 plus 29 plus 17 per cent, successively, during the period of abundance, totaling approximately 81 per cent of the entire infestation. The actual host mortality, however, was lower than this figure, since the mortality in the early stages of the parasite has not been taken into account.

FIG. 9.—Popillia parasitized by Centeter, in process of packing for shipment to the United States, 1921

COLLECTION AND SHIPMENT

Very extensive collections (fig. 9) of parasitized beetles were made at Sapporo and Koiwai in 1921 and at the former place only in the following two years. Two hundred and ninety-six thousand were secured during this period. As many as 200 men, women, and children

were engaged in collecting at one time. They were shown specimens of the beetle bearing eggs of *Centeter cinerea* and offered 50 sen (25 cents) per hundred for all brought in. In this way as many as 56,000 were secured in a single day during 1922. Since the beetle is killed within six days after the deposition of the egg it was evident that the feeding period of the host itself was very short, and consequently elaborate arrangements for providing food in the cages were not necessary. Cardboard boxes of about one-third cubic foot capacity were used, each being filled loosely with grape or Polygonum foliage, and from 500 to 1,000 beetles were placed therein. These boxes were set aside without further attention for six days, after which they were opened and the beetles still alive were permitted to escape, as the parasites of these had died without effecting the death of the

FIG. 10.—*Spalangia* sp., a parasite of *Centeter cinerea*

host. Had these beetles been permitted to die in the boxes their putrefying bodies would have exerted a detrimental effect on the larvæ and puparia present. It was found that the foliage in the boxes maintained a fairly high moisture content for a considerable period, so that pupation was effected without difficulty. Upon the completion of this the dead beetles containing the puparia were screened out and packed in moderately moist sphagnum moss for shipment to America.

From the shipments thus far made a large number of adults have been obtained. In 1922, however, only 700 adult flies were reared at the Riverton laboratory, but in 1923 approximately 7,000 were secured. These were liberated in the field, and beetles bearing Centeter eggs were found one week later. This colony survived the winter in good condition, for in the summer of 1924 beetles bearing eggs were found 2 miles from the point of the previous year's liberation, or covering an area of approximately 12 square miles.

SECONDARY PARASITISM

In the large shipment of *C. cinerea* material forwarded from Japan in 1921 there was contained a considerable infestation of several species of chalcid secondaries, the more important one being *Spalangia* sp. (fig. 10). The first trace of this hyperparasitism was found at Koiwai in an examination by dissection of a portion of the Sapporo-collected material shortly prior to shipment. The laboratory at Riverton, N. J., was immediately advised of this

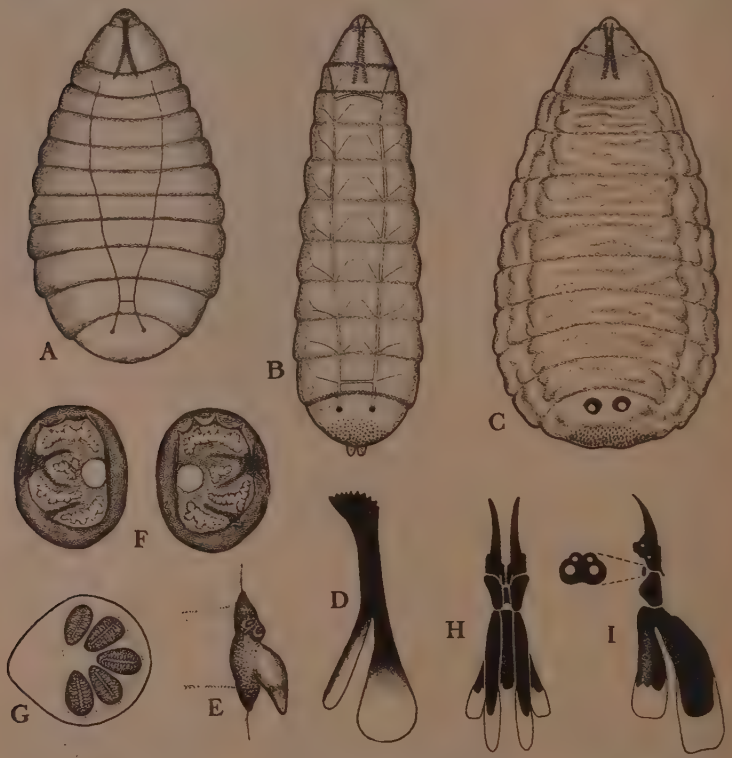

FIG. 11.—*Centeter cinerea:* A, first-stage larva; B, second-stage larva; C, third-stage larva; D, mouth parts, first-stage larva, lateral view; E, caudal spiracle, second-stage larva; F, caudal spiracle, third-stage larva; G, right anterior spiracle of same; H, third-stage larval mouth parts, dorsal view; I, same, lateral view

development and it was thus made possible to guard against the escape of the species at the time of emergence. The proportion of the puparia attacked in the two main shipments was approximately 10 per cent.

LIFE HISTORY OF CENTETER CINEREA

Hatching of the egg.—After having been laid, usually on the thorax, the egg develops rapidly, and the young larva is fully mature within 36 to 48 hours after oviposition. Unlike many tachinids this species does not hatch externally, but while still inside the eggshell drills

directly downward through the shell into the body of the host. The penetration of the heavy exoskeleton of *Popillia japonica* by so minute a larva is made possible by a modification in the structure of the tip of the mouth parts (fig. 11, D), which is provided with a row of heavy teeth forming a "rasper" by means of which a hole sufficiently large to permit of the passage of the body is made (fig. 12). The process of penetrating the thoracic wall is complete in 6 to 12 hours after its commencement, provided the temperature is reasonably high.

FIG. 12.—Cross section of egg of *Centeter cinerea* upon the heavily chitinized thoracic wall of *Popillia japonica*, showing the aperture made by the first-stage larva in entering the host body

In the case of eggs deposited on other parts of the body, the larvæ in many cases are unable to effect entrance into the body proper. About half of those deposited ventrally on the thorax fail to penetrate on account of the extreme thickness of the exoskeleton at this point. When placed on the elytra few ever reach the body cavity, for having passed completely through the wing cover, they still lie free on the outer surface of the body. Under these conditions they are unable to drill the necessary hole in the derm and soon succumb. Eggs are occasionally placed upon the legs, and of these the ones placed upon the femora are capable of reaching the body cavity, but those on the tibiæ very seldom do.

The larval stages.—In considering the development of the larvæ from the time of hatching onward, only those developing from eggs placed dorsally on the thorax will be dealt with, since this is the normal position. After penetration of the thoracic wall the young larvæ move about somewhat in the thoracic cavity, and the first molt takes place in this portion of the body. Migration to the abdomen occurs almost immediately after the first molt. In the second stage the spiracles are each equipped with a strong hook (fig. 11, E), and dissections of living beetles containing these larvæ indicate that the hooks serve to perforate and to attach the body temporarily to one or more of the numerous air sacs within the host, and that respiration is effected in this way.

After leaving the thorax the larva gradually works its way back to the tip of the abdomen, after which it turns and once more enters the thorax. The death of the female host occurs just prior to this point. The entire contents of the thorax are then consumed, the larva turns once more, enters the abdomen, and completes its feeding, usually devouring the entire body contents with the exception of some of the fully mature eggs. In the case of male beetles the second molt of the parasite takes place in the abdomen rather than in the thorax, and death of the host does not occur until the third stage is reached. Pupation takes place within the dead body of the beetle, with the head closely appressed to the tip of the abdomen. This occurs about four days after the death of the host.

Molting of both of the early stages takes place by means of an anterior split in the derm rather than by its sloughing off in fragments, as occurs in many tachinid species. The process is very readily observed by placing living larvæ of various stages in a normal saline solution, in which they will live for a considerable length of time.

At first it might be supposed that the males, having a smaller quantity of food material in the body, would succumb to the attack of the parasite more quickly than the females, but this is not the case. The vital organs of the female are attacked sooner than those of the male and consequently death takes place earlier. A series of females under observation averaged 5.2 days from the time of deposition of the egg until death, whereas the males averaged 5.8 days, with a maximum of 6 days for the former and 8 days for the latter.

The time elapsing between oviposition and the pupation of the parasite was 9.1 days for the females and 9.2 days for the males. It is thus seen that the early stages of this parasite are of extremely brief duration. Shortly prior to its death the beetle host buries itself in the soil and thus the parasite, being within the body, is provided with an air-filled chamber within which to pass the dormant period.

The number of eggs deposited upon single beetles led to observations to determine if it were possible for more than a single individual to reach maturity in each host. In the case of excessive duplication of oviposition—that is, with five or more eggs upon the body—it was found by dissection that the surplus larvae were killed in the second stage, whereas with less than that number the mortality occurred largely in the third stage. Two mature larvae have been found in a single beetle, but the weaker of these is usually killed and the other pupates normally. In the laboratory, occasional instances have been noted of two puparia being produced in a single host.

Pupal stage.—Of a quantity of beetles collected bearing only one parasite egg each, 88 per cent eventually produced puparia, the remaining 12 per cent having died in the egg or first larval stage, and before any effect was produced upon the host. This loss resulting from mortality in the early stages is largely offset in the field by duplicate oviposition.

The mature fly.—The duration of the pupal stage averages about 10.5 months, and emergence is effected during the latter part of June at Sapporo. The cap of the puparium is broken off, the dorsal portion of the two caudal segments of the beetle abdomen pushed away, and the fly then works its way up through the soil into the open air. Emergence occurs largely during the early morning hours. Mating has not been observed.

Feeding occurs principally in the afternoon upon aphis honeydew and at the nectar glands of various plants, particularly itadori (*Polygonum reynoutria*). At Sapporo large numbers of males and some females were collected on aphis-infested elm foliage. In the breeding cages honey or sugar water served very satisfactorily as food materials.

In the field the flies were found most commonly along roadsides, pasture borders, and streams, where more or less wild vegetation was present and where cultivation did not interfere with the puparia in the soil. In general it may be said that conditions suitable for the development of the host are also nearly ideal for the parasite. The degree of parasitism in the field was unusually uniform throughout all the types of habitat favored by the beetle.

Oviposition does not occur extensively during the cool days frequently prevailing in mid-July in Hokkaido, or upon the days of unusually high temperatures. The optimum condition for oviposition is a temperature of about 85° F. with a fairly high humidity

and the sky somewhat overcast. Under these conditions the beetles remain upon the foliage throughout the day, in contrast with their disappearance about noon on days when the temperature is high and the sunlight intense. This gives the fly a greater opportunity to oviposit, and its own inclination to continue this throughout the day rather than to remain quiescent on the foliage results in a much increased deposition of eggs.

The manner of oviposition is very unusual in that it leads to the placement of the egg on a restricted portion of the host body. In case the beetles attacked are feeding singly upon the foliage they take alarm immediately a fly alights in the vicinity, and a closer approach leads them to drop to the ground. For this reason oviposition normally takes place upon mating pairs, since these do not take alarm so readily. The female fly may stand about on the leaf for some time, apparently watching the beetles, after which she makes a dash for the pair, running diagonally across the thorax of the female and pausing only for an instant to place an egg thereon. About 98 per cent of all eggs laid are so placed and, under normal conditions such as prevail at Koiwai, about 85 to 96 per cent are upon female beetles. This has a very important bearing upon the effectiveness of the parasite.

FIG. 13. Reproductive organs of female *Centeter cinerea*

Oviposition occurs at times on other parts of the beetle body. Occasionally a fly will approach the host from the rear, in which case the egg is placed upon the elytra, or from the side, when it may be laid on one of the legs. The greater proportion of misplaced eggs, however, are ventrally on the thorax, these having been so placed by oviposition through a hole in the leaf. Instances have been observed of female flies alighting directly upon the beetles from flight, and here there is no uniformity in the position of the egg. Occasionally a pronounced struggle may take place between the fly and the beetle, and both may drop to the ground. In this event, however, the attempt to oviposit is seldom successful.

The rate and duration of oviposition under laboratory conditions were observed in a series of 24 females collected in the field sufficiently

early to preclude the possibility of any extensive oviposition having previously taken place. The greatest number of eggs secured from a single individual was 62, and the maximum for one day 21. None of the females lived longer than eight days in captivity, this certainly being much less than the normal under field conditions. In the field, oviposition ranges over a period of about two weeks, and exceeds 100 eggs.

Dissections of gravid females showed that each of the large, spherical ovaries (fig. 13) consisted of an average of nine follicles each. The number varied from 6 to 11, and in the greater propor-

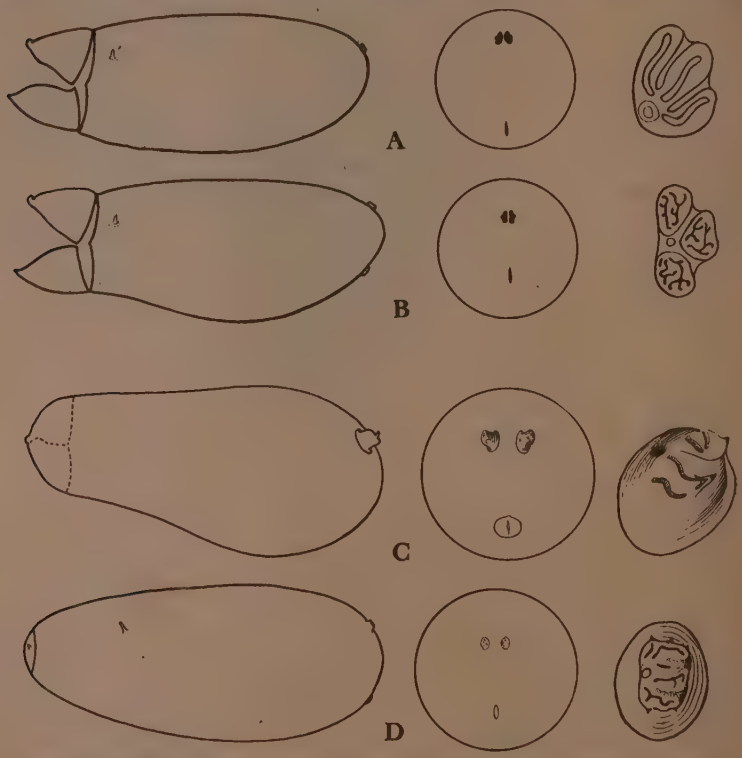

FIG. 14.—Dexiid and tachinid puparia, showing their distinguishing characters: A, *Dexia ventralis;* B, *Prosena siberita;* C, *Ochromeigenia ormioides;* D, *Centeter cinerea*

tion of individuals was the same in each ovary. An average of 11 mature eggs was found in the gravid females examined. A single egg was always present in the ovarian sac, one in one or both of the ovarian tubes, and a varying total in the follicles. Each follicle normally contains one fully developed egg, one slightly more than half size, and a series of buds of diminishing size

It appears from the observations made that a follicle is capable of developing a single egg daily, and that consequently the number of follicles present determines the potential daily rate of oviposition, those with a total of only 14 follicles being capable of producing only

that number of eggs, whereas one with 22 follicles yields a correspondingly greater number This conjecture is borne out by the subsequent examination by dissection of the ovaries of the particular females under observation.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF CENTETER CINEREA

First-stage larva (fig. 11, A).—Length approximately 0.7 mm.; color white. Mouth parts modified for rasping, as shown in D. Visible tracheal system consisting of two longitudinal trunks; caudal spiracles small and inconspicuous.

Second-stage larva (fig. 11, B).—Posterior spiracles fairly prominent, with a hooklike projection, as shown in E. The main tracheal trunks fairly heavy, with two main transverse commissures connecting them at the fourth and eleventh segments. Posterior half of last segment and hind margin of the eleventh segment bearing numerous short but stout spines. There are two prominent lobes at the anal opening.

Third-stage larva (fig. 11, C).—Length 8 to 10 mm.; color white. Mouth parts as shown in H and I. Anterior spiracles with five openings, as in G. Posterior spiracles as in F. Posterior area of the caudal segment bearing numerous stout spines.

Puparia (fig. 14, D).—Length 5 to 7 mm.; color brown, surface striate, reflections dull. Shape elongate-oval. Thoracic spiracle present, in the form of an elevated tube; posterior spiracle as in D.

OCHROMEIGENIA ORMIOIDES Townsend

GENERAL OBSERVATIONS

Adults of *Ochromeigenia ormioides* were first obtained from *Popillia japonica* collected at Yokohama in June, 1921 (fig. 15). It was later found as far north as Koiwai, Japan, and at Suigen, Chosen. The species was first described by Townsend from collections made in Java, and it has also been recorded from western China. As far as known it is a parasite of adult Scarabaeidae only.

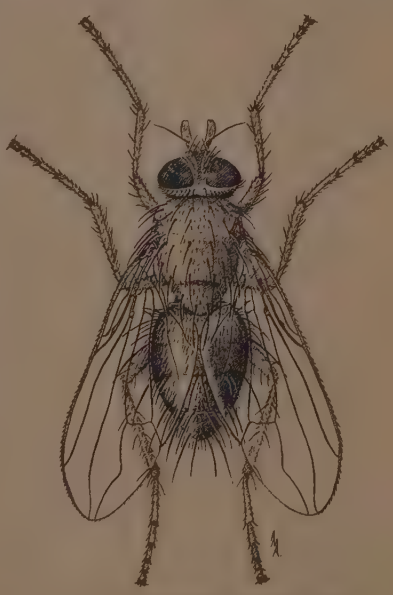

FIG. 15.—*Ochromeigenia ormioides*, female

Apparently this species is more or less periodic in its occurrence on Popillia. In the summer of 1920 empty puparia were found in the breeding cages, which later proved to belong to this species. The number obtained at this time was small, indicating an exceedingly low percentage of parasitism. In 1921 collections yielded less than 1 per cent of parasitized beetles. However, collections in 1922 in the vicinity of Tokyo and Yokohama ran as high as 35 per cent, and this was followed in 1923 with a 6 per cent parasitism.

Ochromeigenia ormioides has three broods of adults per season, the first two of which parasitize Popillia and the third develops in other Scarabaeidae.

SHIPMENTS

Shipments of this parasite were made by collecting large numbers of Popillia in the field and forwarding them without delay. During the ocean voyage this material is held in cool storage at a temperature of 40 to 50° F. The transcontinental shipments are made by express, at normal car temperature, from Seattle, Wash., to Riverton, N. J. Material in refrigeration between these two points has given poor results as compared with material shipped at normal car temperature. On June 27, 1923, 4,000 beetles were shipped from Yokohama, 5 per cent of which were parasitized. Shipments made in 1924 proved successful and from these about 100 adults have been reared and liberated.

LIFE HISTORY

This tachinid is nocturnal in its habits, remaining quiet during the day concealed on the under surface of foliage of low-growing plants

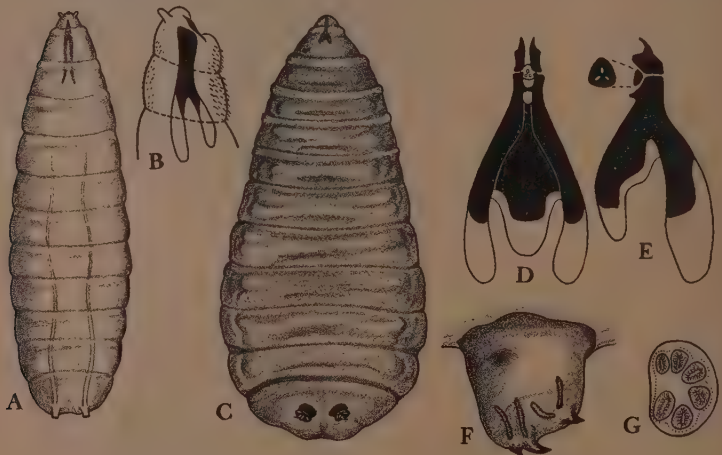

FIG. 16.—*Ochromeigenia ormioides:* A, first-stage larva; B, lateral view of head showing mouth parts, first-stage larva; C, mature larva; D, mouth parts, mature larva, dorsal view; E, lateral view of mouth parts, mature larva; F, right posterior spiracle, mature larva; G, right anterior spiracle, mature larva

and in dense undergrowth. In large cages the flies frequently rest on the upper woodwork 5 feet above the ground. They become active at 6.30 to 7 p. m. during July. On account of their nocturnal habits and their attraction to light it is difficult to observe their normal actions. In nature this fly has been observed to feed on honeydew.

The females deposit larvæ rather than eggs. The exact method of placement of these in regard to the host and the manner of penetration of the larvæ into the host have not been determined. Female flies when in cages with Popillia beetles manifest considerable interest in them by following them about with the antennæ erect and abdomen curved slightly under and forward as if preparing to larviposit. Frequently they will sidestep in a circle around a beetle, investigating it with extended antennæ; then they will run up over the beetle,

approaching it from behind. During this performance they always stand high on their legs and curve the abdomen under and forward. However, careful examinations of beetles after these actions have failed to reveal larvæ upon or within them. Living first-stage larvæ of this fly in one instance were deposited on the glass of the breeding tube, but when transferred to beetles they were soon lost. The first-stage larvæ (fig. 16, A) are very delicate and can not stand much exposure to dry air. Examination of the female flies fails to show any piercing organ by which the larvæ could be introduced into the host. It is possible that the larvæ may enter either through the genital or anal opening, or if they gain access to the softer body wall under the elytra they may penetrate there. The mouth parts of these first-instar larvæ (fig. 16, B) are not specialized in any way as in *Centeter cinerea*.

The puparia of this parasite (fig. 14, C) are formed within the beetle in the same position as those of Centeter, and like it are buried in the ground within the air cavity formed by the body of the dead beetle. The adults when emerging push away the dorsal portions of the last abdominal segments. The period of pupation ranges from 11 to 13 days, with an average of 12 for the first part of July at Yokohama.

The lack of definite data concerning the time of parasitism of the host makes it impossible to determine exactly the length of the entire life cycle. However, adults have been obtained as late as 20 days after the collection of parasitized beetles.

This tachinid has two, and possibly three, generations a season under Yokohama conditions. Adults have been found as early as May 24 in Chosen and as late as September 3 at Koiwai and September 13 at Yokohama.

At Yokohama this fly has also been reared from adults of *Anomala rufocuprea* Motsch. and (*Anomala*) *Phyllopertha orientalis* Waterh., and in Chosen from *Popillia atrocoerulea* Bates and *P. mutans* Newm.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF OCHROMEIGENIA ORMIOIDES

First-stage larva (fig. 16, A).—Length of newly hatched larva approximately 0.5 mm.; color white, pellucid. Sensory papillæ prominent. Mouth hooks present; pharyngeal plates as in B. Visible tracheal system in two parallel tubes; caudal spiracles stalked.

Third-stage larva (fig. 16, C).—Length approximately 9 mm.; color white. Mouth parts as in D and E. Posterior spiracles raised on a disk which bears from three to four hooklike spines; spiracular openings usually four in number.

Puparium (fig. 14, C).—Length 6 mm.; color dark brown, shining. Posterior half swollen. Caudal spiracles elevated and spined as in the larva.

EUTRIXOPSIS JAVANA Townsend

Eutrixopsis javana (fig. 17) was first reared at the Japanese beetle laboratory in June, 1923, from a shipment of *Centeter cinerea* material forwarded from Sapporo, Japan, in 1922, and comprised 210 Eutrixopsis out of a total emergence of 6,734 tachinids, or 3.1 per cent of the total. However, since all the beetles collected for this shipment were those bearing *C. cinerea* only, it is not possible from this collection to make any statement as to the status of Eutrixopsis in Japan, although it is undoubtedly secondary in importance to the species previously mentioned. Whether it deposits eggs which are

indistinguishable from those of Centeter, or produces living larvæ as does Ochromeigenia, is not known.

The life cycle apparently corresponds closely to that of Centeter, only one generation a year being produced.

PROSENA SIBERITA Fabricius

GENERAL OBSERVATIONS

As in the case of *Centeter cinerea* and *Tiphia popilliavora*, the first trace of parasitism by this species upon *Popillia japonica* was obtained at Koiwai, this being in early August, 1921, when four grubs were

FIG. 17.—*Eurizopsis javana*, female

found containing mature larvæ. Breeding experiments were started immediately with adult flies from the field, presumed to be the same species, and the emergence of the adults from the larvæ previously collected later confirmed this conclusion (fig. 18).

Extended investigations on this parasite in Hokkaido revealed it in considerable abundance in several localities, and at Kotoni, a short distance from Sapporo, the field parasitism in 1922 and 1923 was approximately 10 per cent. *Prosena siberita* is found abundantly throughout northern Japan and, according to literature, occurs also in Europe, continental Asia, and the Oriental region, where it has been recorded from Java.

METHODS OF REARING AND COLLECTING FOR SHIPMENT

Considerable difficulty was experienced in breeding this parasite because of the extreme nervousness of the field-collected females under laboratory conditions, resulting in very early death, and the fact that larvæ were produced rather than eggs. Under normal conditions the young larvæ are deposited on the surface of the soil and they then burrow about in search of host grubs, into which they penetrate very quickly.

An examination of gravid females revealed the ovarian sac as containing upward of 800 eggs and larvæ, the number of the latter being variable, ranging from 50 to 300, and located in the terminal

FIG. 18.—*Prosena siberita*, female

portion of the sac (fig. 19). When the wall of this sac was broken with a scalpel or needle the young larvæ were immediately liberated and quickly crawled away. Experiments indicated that larvæ obtained in this way were normal in every respect and were able to penetrate the host and to develop without difficulty. This brought up the possibility of the use of this method in breeding work, the larvæ to be transferred to the host by means of a fine brush. Results were very satisfactory, and practically 100 per cent effectiveness was obtained from these inoculations. At first the half-grown host grubs were placed in individual vials of one-half inch diameter and five or six Prosena larvæ placed upon each, the vials then being filled with

soil to the depth of 1 inch. Many of the larvæ effected penetration within one or two hours after being placed on the grubs, but ordinarily the vials were set aside for 24 hours to insure a maximum parasitism. In 1922 porous-clay blocks were substituted for the vials, each of

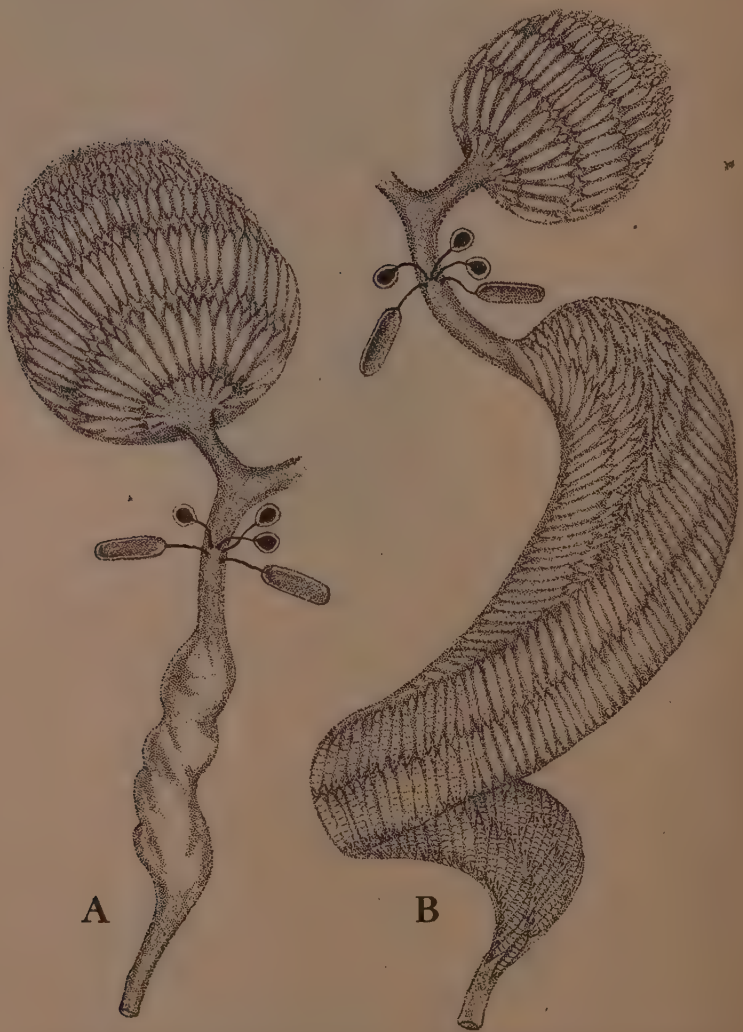

FIG. 19.—Reproductive organs of *Prosena siberita:* A, condition before mating; B, after fertilization, showing eggs and larvae in the distended egg sac

these blocks bearing upwards of 100 cells of a size suitable to accommodate the grubs used. These blocks were more satisfactory in every way and resulted in a considerable saving in time. With this method it was possible for one person to inoculate more than 1,000 grubs per day, provided a sufficient number of flies were available.

In this manner about 800 grubs were inoculated in 1921 and 7,800 the following year. The greater proportion of the flies collected in the field either contained eggs alone or had already deposited their larvæ, so that the average number procured from each fly did not exceed 50.

Upon completion of the field work for the season the parasitized grubs were forwarded to the Riverton laboratory. It was found as a result of these two years' work that the mortality in shipping from Japan and in holding the grubs under laboratory conditions throughout the winter was so great as to render the general method impracticable. Late in 1922 a locality was found in Hokkaido where adult flies were abundant, and this gave promise of a fair percentage of parasitism in the overwintering grubs in the soil. An examination of the field grubs in April of 1923 revealed an average parasitism of 10 per cent. Collections were consequently made of some 11,000 grubs and these were shipped to New Jersey about the middle of June. At the time of collection it was not possible to distinguish between those parasitized and unparasitized, and consequently it was necessary to forward the entire lot. This method of importation resulted much more satisfactorily, since approximately 70 per cent of the parasite larvæ in the shipment yielded adults during July and August, at Riverton.

LIFE HISTORY

The young larva (fig. 20, F), after being deposited upon the soil, burrows about in search of host grubs, being guided probably by the sense of smell. When the host has been found the larva seeks out a crevice or suture in the integument and commences penetration, this being effected in one to two hours. It now lies free within the host body, surrounded by fluids and masses of fatty tissues. No permanent connection for respiratory purposes is made in this stage either with the tracheal system or through the derm. Early in the second stage, however, the caudal spiracles are attached to a main tracheal trunk near the thoracic or first abdominal spiracles of the host (fig. 21, A). The body is directed caudad, and feeding takes place largely in the mid-abdominal region.

The second molt occurs ordinarily in the early spring, and at this time the dark chitinous respiratory funnel appears as a covering of the posterior segments of the larva. In some cases, where the point of attachment is very close to the spiracle, this funnel is dimly visible externally, but dissection is necessary for verification. Development in the final stage is very rapid, and the body of the host becomes more translucent in color, because of the consumption of the fat bodies which normally are present in large masses. The host remains alive and active until practically all of the body contents, aside from the vital organs, are consumed, though during the week preceding death evidence of life is presented only by a spasmodic twitching of the maxillæ or legs.

After the death of the host the Prosena larva tears a hole ventrally in the integument of one of the distal segments of the abdomen, then severs its connection with the respiratory funnel, reverses its position, and completes feeding in the thoracic region. This being

accomplished, and the body contents entirely consumed, it again turns and leaves through the aperture previously made. Pupation takes place in the soil 1 or 2 inches beneath the host remains.

The duration of the various stages in the life cycle is not uniform, and the early stages may be greatly prolonged. The newly deposited larvæ are capable of wandering about in the soil for a week or more in

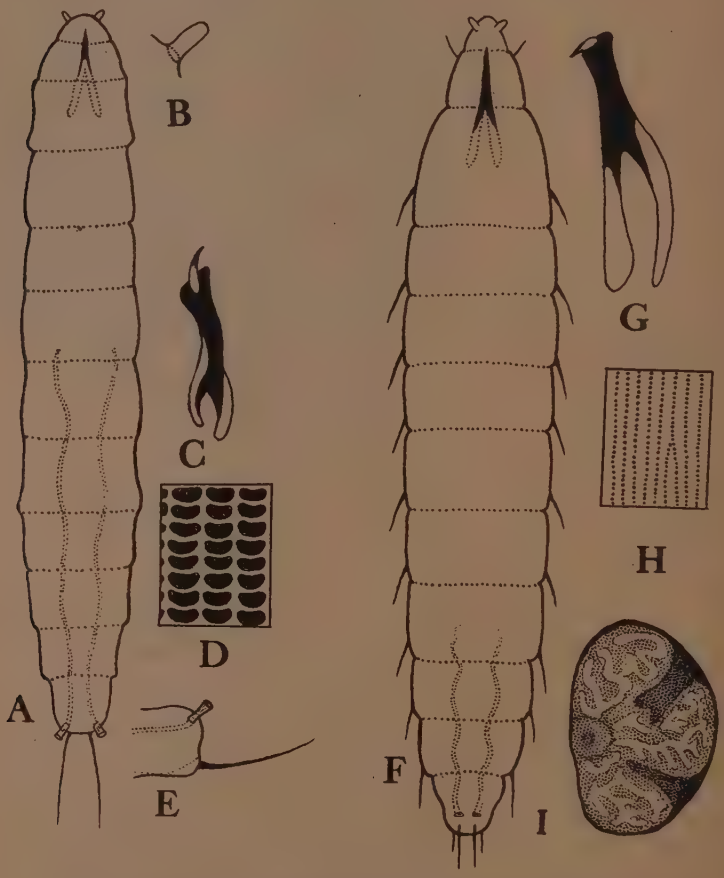

FIG. 20.—A, first-stage larva of *Dexia ventralis;* B, antenna; C, mouth parts; D, enlarged portion of derm; E, lateral view of caudal end of larva; F, first-stage larva of *Prosena siberita;* G, mouth parts; H, enlarged portion of derm; I, posterior spiracle of third-stage larva, *Prosena siberita*

search of the host, and after entrance is effected the further duration of the stage is dependent on temperature conditions and may be extended to the following spring. Usually, however, the first molt occurs during the fall, and the winter is passed in the early second stage. The third stage is relatively short, as determined by dissections of a considerable series of parasitized grubs during May and June.

At Sapporo the pupation of the earlier individuals begins about the first of July and ranges over the entire month. Under high temperature conditions the pupal stage averages about 22 days, whereas at Sapporo it may extend to 30 days in case the weather is cool. Emergence occurs during the early morning hours.

HABITS OF THE ADULT

The adults are somewhat crepuscular in habit, being active on bright days largely about sunset, but at Koiwai the greatest numbers were always to be found during the rainy periods which occurred almost daily, and practically all collections were made under these conditions. Heavy rains, however, caused them to remain quiescent on the under sides of surrounding foliage. Feeding takes place largely at the blossoms of two umbelliferous plants (*Seseli libanotis* and *Patrinia scabiosaefolia*).

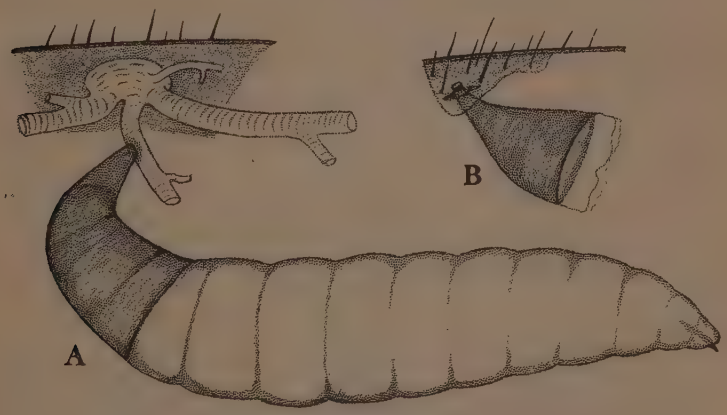

FIG. 21.—A, larva of *Prosena siberita* in situ, with tracheal funnel attached to trachea of host; B, tracheal funnel of *Dexia ventralis* penetrating the derm of host

Mating is effected largely upon the blossoms of these food plants or upon surrounding foliage and at times upon tree trunks. The pairs may remain in copula for a considerable period, and at this time may be captured very readily. Single individuals are very active and take alarm quickly.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF PROSENA SIBERITA

First-stage larva (fig. 20, F).—Length of newly hatched larva approximately 1 mm.; color white. Mouth hooks present; pharyngeal plates as in G. Sensory papillæ prominent. Derm finely striate. Body segments each bearing a strong lateral bristle; caudal setæ four in number. Posterior spiracles sessile.

Third-stage larva (fig. 21, A).—Length 14 mm.; color white. Caudal spiracles as in Figure 20, I. Tracheal funnel always attached internally to the large tracheal trunk of the host near the thoracic or first abdominal spiracles.

Puparium (fig. 14, B).—Length 10 to 12 mm.; color dark brown, reflections dull, surface striate. Posterior spiracles divided into three lobes bearing the branchlike design of the former tracheal openings; thoracic spiracle present in the form of an elevated tube.

DEXIA VENTRALIS Aldrich

Dexia ventralis (fig. 22) is the most common of the dexiids of Chosen, and was first found shortly after the commencement of investigations in that country in late May, 1922. Experiments with it upon grubs of *Popillia japonica* indicated that it would develop satisfactorily in that host, and, consequently, further studies were made upon its biology.

In distribution, this species covers all of Chosen and also the plains area of Manchuria, which latter was scouted during the summer of

FIG. 22.—*Dexia ventralis*, female

1923; but it is most common in the central portions of the former country. It is also recorded from the Malayan region. Practically all of the breeding and life-history work was done at Suigen, Chosen.

No shipments of this species have been made to America as yet on account of the necessity of first determining certain factors in its biology which have an important bearing upon its potential value under the changed conditions. These various factors will be discussed in detail later. The earlier observations indicated only one generation per year, and since the adults appeared in late May and disappeared within one month it was naturally concluded that the

parasite could not be of value against *P. japonica* in America. The 1923 investigations, however, revealed two additional generations each year, and this fact changed the status of the species markedly as regards its potential value.

LIFE HISTORY

In a consideration of the life history of Dexia, the young larvæ produced by the spring generation of females may be taken as the starting point. These burrow about in the soil in search of hosts in exactly the same manner as Prosena, and penetration is effected in the same way. This occurs largely on the dorsal portion of the anterior half of the body. Here the analogy between the two species ends, however, for the young larva upon penetration attaches its caudal end to the aperture in the derm of the host and thus sets up immediately respiratory connection with the outside air. (Fig. 21, B.) The first molt occurs within a few hours thereafter, and consequently the dark-colored respiratory funnel is distinctly visible externally on the same day that the host is entered. This is in marked contrast to the attachment of the respiratory funnel of Prosena in the early second stage to the tracheal trunk of the host, the funnel of which is not visible until the host is almost entirely consumed. Feeding during the early stages is largely upon the fluid contents of the host body, and in the later stages upon the fat bodies, and finally on the vital organs. During this period the parasite body lies with its head directed caudad with respect to the host.

Growth in all of the larval stages is very rapid, the host being dead and the body contents entirely consumed within 10 to 15 days after penetration. A hole is cut ventrally in the wall of the abdomen by the mature larva after the host is killed; it then turns about and feeds in the thoracic regions, and finally emerges and pupates exactly as does Prosena. The pupal period covers seven to nine days. Under field conditions only a single individual reaches maturity in each host, though many grubs have been collected which contained 20 or more first-stage larvæ.

Second generation

The midsummer generation of adults appears during the period beginning about July 25 and extending to August 20, though the greatest numbers are present during late July. The lengths of the various stages correspond very closely to those of the preceding generation.

Third generation

The first of the fall brood of adults appears in the field about September 1, and a maximum abundance is attained by the middle of that month, although females may still be found commonly as late as the middle of October. The temperature during the latter part of this period is very cool, being often below freezing in the early mornings. The progeny produced by these females enter the host and pass the winter in the second larval stage. On account of the lower spring temperatures, the pupal stage is somewhat longer than in the other two generations. The first adults appear about May 22 and persist not later than the middle of June.

Alternation of hosts

The parasite larvæ of the second stage, which carry the species over the winter, are found in three host species, *Miridiba koreana* N. and K., *Popillia castanoptera*, and *Phyllopertha* sp. An examination of field-collected grubs on October 10 revealed the following condition: *Anomala* spp., all Dexia larvæ either dead or lost in molting; *Phyllophaga* spp., all Dexia larvæ either dead or lost in molting; *Miridiba koreana*, all Dexia larvæ in second stage, healthy; *Phyllopertha* sp., all Dexia larvæ in second stage, healthy; *Popillia castanoptera*, all Dexia larvæ in second stage, healthy; *Popillia atrocoerulea*, all Dexia larvæ dead.

The three species which contained living parasite larvæ at this time naturally included the true host. *Popillia castanoptera* may be excluded, since its time of pupation is too late for this generation of parasites. Although it can not be stated as yet with certainty, the available data indicate that *Miridiba koreana* is the major if not the only host of the overwintering generation.

The host of the following generation is also not positively known, but a consideration of the species of beetles of proper size pupating about midsummer points to *Popillia castanoptera* and *P. mutans* as the more probable species.

The third generation of adults emerges exclusively from larvæ of Serica, which latter pupate late in the fall and pass the winter in the adult form in the soil. An examination of field-collected grubs obtained August 12 to 27, 1923, gave the following data:

	Number examined	Number parasitized	Percentage of parasitism
Anomala spp. (third stage)	3,647	51	1.4
Phyllophaga spp. (second stage)	8,545	863	10.1
Serica spp. (third stage)	935	129	13.8
Popillia spp. (third stage)	137	0	0

The counts of parasitized grubs were based upon the funnels visible through the derm, and consequently a portion of the parasites may have been dead at the time of collection without this fact being noticed. Dissections of a representative series were made and the living Dexia larvæ found to be in the second stage, though those in Serica seemed to be further advanced, and a few had attained the third stage. All the remaining parasitized grubs were set aside in trays for development and were again examined on August 27. Of the 863 Phyllophaga grubs, 747 were still in the second stage, and dissections showed all parasite larvæ contained in them to have been killed in the first or early second stage, whereas 116 grubs had transformed to the final stage and had rid themselves of all evidence of parasitism in the process. Among the Serica grubs 82 were still alive and contained third-stage Dexia larvæ, whereas 37 had already died and yielded puparia.

Rare instances have been observed of this species reaching maturity in field-collected pupæ. In one instance a Serica grub containing a late second-stage larva was able successfully to pupate

and later develop into an imperfect beetle. Another succeeded in freeing itself from a second-stage parasite larva 3 mm. in length, but later died from mechanical injuries incident to the withdrawal of the larva through the aperture in the dorsum of the thorax. It is thus seen that the attachment of the parasite by means of its respiratory funnel to the derm of the host larva is very strong, since it is able to withstand the strain exerted by the drawing of the body through a relatively small opening in the newly formed derm of the pupa.

First-stage larvæ from the adults of the first generation were used in a series of experiments upon grubs of *Popillia japonica*. All of the latter which were available were in the advanced third stage and preparing to pupate. An excessive number of planidia effected entrance into each host, as was evidenced the following day by the many respiratory funnels visible underneath the derm. Within a very few days most of the grubs pupated and the parasite larvæ were able to sever their connection with the respiratory funnel, and remained with the caudal end of the body protruding externally. A few maintained the attachment and held the cast skin in position upon the pupal body.

Some of the parasitized larvæ died from injuries incident to excessive superparasitism, and in these instances the third-stage parasite larvæ detached themselves from the funnel and forced the caudal end of the body out through the aperture in the derm. These host grubs then assumed a somewhat mummified condition, but this may be attributed to bacterial and fungus action rather than to any development in relation to the parasite itself. Feeding was continued on the dead body and pupation took place normally and just outside the host remains, which had not been entirely consumed.

The necessity, under Korean conditions, for these different hosts within which the successive generations may develop is due to the fact that the larvæ can reach maturity only in grubs which themselves are undergoing histolytic action preparatory to pupation. This physiological change seems to provide the necessary stimulus for development, a condition which is known to exist in respect to many other parasitic insects, and without which the parasite larva either remains in the early stages or dies. The writers' observations indicate the above state of affairs to exist in all the species of Dexiidae studied; and, although the time of pupation of Prosena would seem to contradict this assertion, the fact is that the presence of the parasite larva in the grub body tends to prevent actual pupation but permits the host to live several weeks or a month beyond the time of normal transformation.

Habits of the adult.—Mating has not been observed in the field, but presumably takes place shortly after emergence. The males appear a few days prior to the females. In the laboratory mating was induced very readily in glass vials or test tubes of 1-inch diameter, and the duration of copulation was normally 10 minutes.

Feeding also has never been observed under field conditions, in spite of the extensive observations made throughout the periods of adult abundance. Unlike Prosena, which has a long, lancetlike proboscis fitted for penetration to the deepest nectar glands of certain blossoms, this species has a very short, fleshy proboscis and is therefore probably a feeder upon honeydew of aphids and other

insects. In the laboratory feeding took place very satisfactorily upon honey or sugar water, and individuals were kept alive for one month under these conditions.

Dexia is decidedly crepuscular in habit and is therefore active largely during the period about sunset and at other times when the sky is overcast and direct sunlight is absent. One of the best places found for the collection of adults of this species was a young pine forest at the summit of a hill near the experiment station at Suigen, Chosen. Here they appeared abundantly resting upon the foliage of the broad-leaved oak, apparently preferring this almost to the exclusion of other types of foliage.

Unlike Prosena, which deposits larvæ exclusively, Dexia may at times produce eggs, which have a variable period of incubation externally, depending upon the extent of development attained prior to deposition. Some eggs kept under moist conditions in Petri dishes required two days' incubation, although the average period was much shorter. By far the majority, however, hatch within the ovarian sac and the eggshell is extruded with the larva, in this respect differing also from Prosena, which largely retains the shells.

The larvæ are very evidently scattered promiscuously over the surface of the soil, but observations in the collection of parasitized grubs would seem to indicate that they are deposited in some numbers at each point rather than singly. It was frequently found that grubs within an area of about 1 square yard were very heavily parasitized, whereas those surrounding this area contained practically no parasites, and that these spots of heavy parasitism recurred in greater or less abundance throughout the zone of collection. No locality was found where the parasitism was at all uniform throughout the entire area.

PROBABLE VALUE OF DEXIA VENTRALIS AGAINST POPILLIA JAPONICA IN AMERICA

A consideration of the life history of *Popillia japonica* and of *Dexia ventralis* in Chosen still leaves open the question of the latter's ability to increase to a point where it will be of value as a check upon this particular host. Climatic conditions in New Jersey and Pennsylvania are not markedly different from those in Chosen, and consequently may be regarded as a minor factor. The major difficulty is the occurrence of three full generations of the parasite per year under normal conditions, probably only one of which could be upon *P. japonica*. It appears probable that the overwintering forms would be contained in grubs of this host, and if such is the case the emergence of the first brood of adults would be delayed until the middle of June, as against a month earlier in Chosen, and the larvæ produced by these females would be able to parasitize such grubs as had not yet pupated. This, however, calls for the utilization of the one host species to carry two generations of the parasite, a condition not conducive in this case to the attainment of maximum numbers of the latter. The following generation must of necessity be upon some scarabaeid grub of proper size which pupates about the first of September. This condition is fulfilled principally in the subfamily Sericinae. Full data are not as yet available as to what may be had in the infested regions in this regard, but the general outlook is not good for the development of this species to an important position in the parasite series under course of establishment in America.

CHARACTERS FOR DETERMINING THE IMMATURE STAGES OF DEXIA VENTRALIS

First-stage larva (fig. 20, A).—Length of newly hatched larva approximately 1 mm.; color white. Mouth hooks present; pharyngeal plates as in C. Sensory papillæ prominent. Derm minutely sculptured with rows of reniform elevations. Posterior spiracles stalked. Two long caudal setae.

Third-stage larva.—Although this is not illustrated, the nature of the caudal spiracles may be understood from those of the puparia. Tracheal funnel always attached to the derm of the host (fig. 21, B).

Puparium (fig. 14, A).—Length 8 mm.; color dark brown, reflections dull, surface finely striate. Posterior spiracles divided into three lobes, each bearing an elongate depression of the former tracheal openings.

CAMPSOMERIS ANNULATA Fabricius

GENERAL OBSERVATIONS

Campsomeris annulata (fig. 23) was found rather infrequently at Suigen, Chosen, in August, 1923, and during the following month five

FIG. 23.—*Campsomeris annulata*, female

females were captured in the field. Specimens of both sexes were submitted to S. A. Rohwer, of the Bureau of Entomology, who made the determination. One specimen in the collection of the agricultural experiment station at Suigen bears the name *Elis ventralis* Smith, and under this name is reported by H. Okamoto to be common on Quelpart, a volcanic island lying a short distance off the southeastern point of Chosen. The species is also recorded from Japan as well as oriental Asia.

Experiments were conducted to determine the true host, since the size of the females was such as to permit of development on grubs of *Popillia japonica*. In the first experiments eggs were laid freely upon grubs of *Anomala* sp. and upon *P. atrocoerulea*, and later when mature grubs of *P. japonica* were obtained and supplied to the Compsomeris females, oviposition took place as readily as upon the two species previously mentioned. Considering the distribution of

the species, its habits, life history, etc., it appears probable that Anomala is the true host of the late generations, although Popillia serves equally well when present.

LIFE HISTORY

Since *C. annulata* has been under observation for only a portion of one season, it is not possible at this time to present a complete account of its life history. In breeding experiments it was found that the methods used for Tiphia were not at all satisfactory, the females refusing to oviposit under the conditions provided. When placed in glass jars of about 1-quart capacity, which had been nearly filled with well-packed soil, no difficulty was experienced. It appears necessary to provide these large breeding jars and to have the soil firmly packed in order that a well-defined cell may be formed by the grub, this latter apparently being necessary to the wasp at the time of oviposition. It appears also that the grub after being paralyzed is moved about in the soil to a considerable extent by the wasp before the egg is laid. In the field this behavior may be due to the need of the parasite to provide temperature and humidity conditions for her progeny more favorable than are present in the grub cell, which may be close to the surface and very dry.

It has not thus far been possible to obtain oviposition under conditions which would permit of uninterrupted observation of the act, but stinging is probably accomplished in the same manner as by Tiphia. However, the paralysis effected is permanent rather than simply for the period required for oviposition, and consequently the paralyzed grubs could be placed in small depressions in moist soil and left without further attention until the formation of the cocoon.

The egg is normally placed medially on the ventral surface of the third or fourth abdominal segment, standing perpendicularly, with the posterior end adhering lightly to the derm. The attachment is very insecure, and in case the host grub is imperfectly paralyzed is usually rubbed off by the slightest movement of the body.

Hatching is effected by an irregular break in the chorion of the anterior end of the egg, and through this aperture the head and thoracic segments of the young larva emerge. The head is then lowered and the feeding puncture made on the median line of the next segment caudad. This feeding puncture is in reality a pronounced hole made in the derm, and is sufficiently large to permit the head to become completely buried within the body. An exudation of the body fluids of the host takes place, and the "neck" of the larva is encircled by a quantity of this fluid external to the puncture.

Molting occurs several times, and feeding continues at the same point throughout all the stages, after which the entire body contents are consumed. The cocoon is then spun, consisting of a dense mass of reddish-brown strands loosely woven together on the outer surface but compact within. It is not noticeably differentiated into layers, as is the case with that of Tiphia.

The egg and larval stages prior to the formation of the cocoon cover periods of only 2 and 5 days, respectively, and the time passed within the cocoon only 33 days for the single male thus far reared. This, however, was under relatively low temperature conditions, and is doubtless considerably shortened during mid season. The females

produced from eggs laid August 16 remained in the pupal stage until the following spring. From these fragmentary data it may be surmised that, under optimum conditions, a generation may be produced each six weeks, and that the number of generations per year will depend on the ability of the parasite females to find suitable grubs upon which to oviposit at all times during the season.

CONDITIONS AFFECTING THE DEVELOPMENT OF CAMPSOMERIS IN AMERICA

Since *Campsomeris annulata* is being introduced into America as a parasite of *Popillia japonica*, it is natural that consideration should be given to such factors as are likely to affect its development and increase there. The size of the adult wasp indicates that it is able to produce normal-sized progeny only upon Popillia grubs which have reached full maturity, and since these are not present in large numbers during the summer months, two courses of action are open to the parasite. One of these is to seek out some other host upon which to produce the midsummer generation, and the other is for the females to prolong adult life until suitable Popillia grubs become available in the fall. Both of these alternatives would result in decreased effectiveness against the major host as measured by the potential rate of increase, and although this may be unavoidable, the parasite may still be of considerable value in its early spring and late fall generations and in conjunction with the various species of Tiphia may contribute to the sum total accomplished by the grub parasites.

TIPHIA POPILLIAVORA Rohwer

GENERAL OBSERVATIONS

Tiphia popilliavora (fig. 24), a parasite of Popillia grubs, was first found on August 20, 1920, at Koiwai in the identical place where *C. cinerea*, the tachinid parasite of adult beetles, had been located a week previously. Seven species of Tiphia were on the wing at that time and fed largely on the same blossoms. These species were successively tested upon grubs of *P. japonica*, and *T. popilliavora* was found to oviposit readily. Subsequent field observations proved the species to be restricted in this locality to the above host alone. Specimens were forwarded to the United States National Museum for examination and have been described by Rohwer as a new species under the above name.

Investigations throughout the seasons of 1920–1923, inclusive, in the various parts of Japan have failed to reveal this scoliid in any abundance other than in the very restricted locality in which it was originally located. However, late in 1923 it was found to occur in small numbers at Suigen, Chosen. Here it was determined experimentally to be parasitic upon *Popillia castanoptera* and *P. atrocoerulea*, the former being the more common host. The major investigations and breeding work were confined to Koiwai entirely and covered the three years 1920 to 1922, inclusive.

T. popilliavora is not of major importance in its native habitat, and at no time did the field parasitism exceed 20 per cent. The inability of the species to adapt itself to varying conditions, as evi-

denced by its extremely localized distribution in Japan and Chosen, would tend to limit greatly its possible usefulness in America.

BREEDING METHODS AND SHIPMENTS

Methods of breeding were largely those used by other workers with this group of parasites. Single females were placed in 3-ounce tin salve boxes which had been filled with soil and into which two or three Popillia grubs had been placed (fig. 25). As food for the wasp a drop of honey or sugar water was placed on a leaf on the surface of the soil. These tins were then set aside for a day and at the end of that time

FIG. 24.—*Tiphia popilliacora*, female

examined, the grubs bearing eggs being removed and fresh ones supplied. Those bearing eggs were transferred to cross-section trays which provided a single compartment for each grub, and in which had been placed soil with a small piece of sod to provide food for the grub during the period elapsing before its death from the attack of the parasite larva. The method of handling grubs parasitized by Tiphia differs from that used with Scolia and Campsomeris, because the grubs are not permanently paralyzed as they are in the latter two genera. During the earlier periods of this work, the soil in the trays was kept fairly moist; but it was found that this was responsible for a considerable mortality among the grubs by fungus attack, and consequently in the later work no moisture whatever was applied, and improved results were obtained.

In using the above method it was possible to carry about 500 females through the entire period of oviposition, and this was nearly the maximum number available in the field. In general, it was found that cocoons could be procured to the extent of about 42 per cent of the original number of ovipositions. The loss of more than

FIG. 25.—Rearing Tiphia, Koiwai, Japan: A, tins in which female Tiphia were kept for oviposition and method of transferring each day to tins containing unparasitized larvæ; B, oviposition tins and cross-section trays in which the parasitized Popillia were kept until the Tiphia had killed them and spun their cocoons

half during the egg and larval periods may be attributed to several factors, among these being mechanical injury to the grubs, fungous and bacterial attack, and finally, but most important, the rubbing off of the first-stage parasite larvæ by the movements of the host grub in the soil.

In 1920 and 1921 all grubs used for rearing purposes were collected in the immediate vicinity of the place where the Tiphia were pro-

cured, but collecting was found to be impracticable there in 1922 and consequently 10,000 were collected in Hokkaido during late July and shipped to Koiwai. The mortality among these grubs during the month from collection to the time of use for breeding purposes was about 50 per cent. A total of 3,350 cocoons have thus far been obtained by the method described above, these being from approximately 10,000 ovipositions. After the formation of the cocoons they were removed from the soil, packed in moss in metal containers, and forwarded to the Riverton laboratory.

LIFE HISTORY AND HABITS

The account of the life history of Tiphia may be started from the egg upon the body of the host grub. This is normally placed ventrally between the fifth and sixth abdominal segments, and half way between the median ventral line and the lateral margin (fig. 26). This position may occasionally vary to the extent of one segment either way. The anterior pole of the egg faces inward. It is always placed in the crevice between the segments and is laid with the ventral surface adhering for its entire length to the derm of the host by means of a mucilaginous material provided by the female wasp at the time of oviposition. This adhesive material darkens considerably in color within one or two days after deposition.

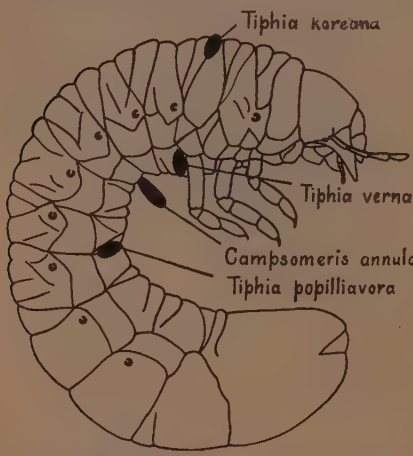

FIG. 26.—A *Popillia japonica* grub, showing the position of the eggs of the four species of Scoliidae parasitic upon it

The duration of the egg stage varies considerably under different temperature conditions. A series of eggs secured at Yokohama averaged 4.5 days, the temperature during that period ranging from a minimum of 80° up to 97° F. At Koiwai, where the breeding work was conducted, the weather was much cooler and the general duration of the stage was prolonged to about eight days.

Hatching is effected by a vertical split at the anterior end of the egg, the head of the young larva being then thrust out and the integument of the host pierced by the mandibles. Feeding begins almost immediately, and as the body becomes distended the break in the shell enlarges and extends down the median line almost to the posterior tip. The shell remains as a ventral pad beneath the larva, and this serves to maintain its attachment to the host.

The first molt occurs very soon and is effected by a dorsal longitudinal split in the skin, beginning at the first thoracic segment and extending almost to the tip of the abdomen. The head is lifted out of the cast skin, moved forward slightly, and reapplied to the host. The cast skin remains adhering to the ventral surface of the body.

Three additional molts occur before the final larval stage is reached, and at each one the head is shifted forward and a new feeding puncture made. The successive cast skins remain in a leaflike form as a pad beneath the body, serving to attach the parasite larva to the host during these stages. There is thus a total of five larval stages, with the eggshell and four cast skins adhering to the final stage. This is shown diagrammatically in Figure 27.

In the last stage feeding is continued at the puncture hole until after the death of the host, when suctorial action no longer suffices and the mandibles are brought into use. The entire body of the host, exclusive of the head and a portion of the legs, is ordinarily consumed, as well as the cast skins of the parasite itself.

The presence of the egg or early-stage larva on the body causes no appreciable inconvenience to the host grub, but as feeding advances it becomes weakened through withdrawal of the body fluids. Death of the host occurs when the parasite larva is in the fifth instar and the formation of the cocoon of the latter takes place within about two days. The duration of the larval stages varies considerably with the temperature conditions, and ranges from 14 days under high temperatures at Yokohama to nearly a month at Koiwai.

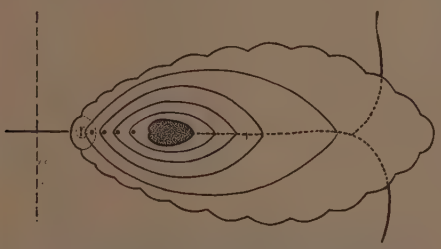

FIG. 27.—Diagrammatic representation of the position of the successive larval stages of Tiphia in situ upon the host, showing the mouth parts remaining in the old feeding punctures. Largest outline represents the fifth and last larval stage

Following the completion of feeding, the spinning of the cocoon is immediately begun, and this takes place in situ in the soil cell of the host. The outer covering is of very loose texture, but the succeeding ones are much more compact. The inner surface is very smooth and firm. The meconium of the larva is cast immediately after the completion of spinning and remains as a hard pad at the posterior end. The dormant period is passed in the larval stage within the cocoon, and pupation occurs only a short time prior to the appearance of the adult.

The first adults appear in the field between August 14 and 18, reaching a maximum abundance near the end of the month and disappearing by the middle of September. The period of gestation covers several days to one week, and, consequently, only about two weeks are available for extensive breeding work. The wasps appear on bright days about 10 a. m., the males slightly earlier, and feeding continues until noon. On cool, cloudy days they are present throughout the day, having been observed feeding as late as 6 p. m.

During 1920 feeding by the adults was confined largely to the blossoms and to the nectar glands on the leaf petioles of itadori (*Polygonum reynoutria*), but in the two years following was almost entirely at the blossoms of two umbelliferous plants, *Seseli libanotis* and *Patrinia scabiosaefolia*. After feeding for the day is complete the females return to the breeding grounds, and there search out

Popillia grubs on which to oviposit. Oviposition occurs largely during the afternoon, but in the warmer periods may continue into the night.

The complete process of egg laying naturally could not be observed in the field, since this takes place entirely underground. In the laboratory, however, visible oviposition was very readily obtained by the use of No. 00 gelatin capsules, a single Tiphia female with a medium-sized Popillia grub being placed in each. Under confinement in such close quarters, comparable to the grub cell in the soil, the attention of the wasp is centered on the grub. She quickly quiets down after being placed in the capsule and soon begins an examination of the grub. She approaches it from the rear, advances over its dorsum until her own head is near that of the host, and then lowers the tip of the abdomen around the side of the body and up between the legs, after which stinging is effected in the ventral thoracic region, usually between the first and second segments. This may be repeated a considerable number of times before the nerve ganglion is reached, after which the grub becomes almost instantly quiescent. The Tiphia then turns to the abdomen and, beginning at the first segment, starts a thorough kneading of the ventral surface with her mandibles. This extends for the entire length of the abdomen but is more thorough on the median segments. From five to seven minutes are devoted to this operation. When it is completed the wasp coils itself transversely about the body in the mid-abdominal region, the mandibles being firmly fastened at the lateral margin, with the body curving over the dorsum and the abdomen extending across that of the host ventrally and almost reaching the point at which the mandibles are attached. The tip of the abdomen is applied to the crease between the fifth and sixth segments and worked back and forth rhythmically for from three to five minutes. This enlarges the crevice somewhat and the rasping of the roughened abdominal tip may also wear away the integument of the host at this point, thus permitting its easier perforation by the young larva. This conjecture is borne out by the fact that, in parasitized grubs, if the body is straightened out between the fingers the point of oviposition is the first to break, and this very readily. The actual deposition of the egg requires only about 15 seconds. It will thus be seen that the entire time elapsing from stinging to the completion of oviposition is from 8 to 12 minutes, but the preliminary examination may prolong the period to half an hour. Within 15 to 20 minutes after it has been stung the grub begins to revive, being then able to move the mouth parts to a certain extent, but movement of the legs and body is not possible within less than 30 minutes. Repeated stinging occasionally brings about the death of the host by mechanical injury.

After oviposition it is a frequent occurrence for the Tiphia female to grasp one of the forelegs between her mandibles and bite it until a break in the derm is effected, or the leg entirely bitten off. This being accomplished, feeding takes place upon the body fluids exuding from the wound. Grubs are frequently found in the field showing this type of injury, and the wound is often accentuated by a blackened area caused by bacterial infection.

When a grub which already bears one egg is attacked a second time, the first egg is almost invariably destroyed by the wasp in the course of kneading the abdominal surface with the mandibles, or broken

during the attempted second oviposition. The grub having once borne an egg in the preferred crevice, or one on each side, is thereafter oviposited upon at a different point, either immediately in front of or behind that position. Where egg laying over a considerable period is confined to a single grub and the host then examined, it is found to bear a pair of oviposition scars on each intersegmental crevice from the first to the last on the abdomen, and only a single egg usually remains, this being the one last laid.

The grubs most preferred by Tiphia for oviposition are those in the early or middle third stage, for after they pass to the more mature form the body becomes thickened and firm, and thus apparently presents mechanical difficulties to stinging and egg laying. Such grubs are from eggs laid the previous season, and it was only with great difficulty that wasps were induced to oviposit upon them. In the field during early September the grubs from eggs of that season were largely in the second instar, and collected grubs of this stage often bore Tiphia eggs and larvæ. Manifestly, grubs in this stage were unable to provide sufficient food to bring the parasite larvæ to maturity, and in many cases observed the resulting cocoons were little larger than those of an average-sized Apanteles. The larvæ in these cocoons usually die shortly after the formation of the cocoon. This willingness of the species to oviposit upon grubs of too small size to bring its progeny to maturity indicates a lack of perfect adaptation to a one-year cycle of the host, because of the improper time of emergence for a wasp of this size.

The rate and duration of oviposition in this species were determined in a series of 28 females collected in the field on August 19, which was very nearly the first date upon which adults appeared, and consequently it is reasonably certain that little or no egg laying had taken place up to that time. Records of the 10 best females are given in Table 2, and this is felt to represent very nearly the normal condition in the field.

TABLE 2.—*Oviposition records of 10 females of Tiphia popilliavora*

Female No.	August											September										Total
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9	10	
1	3	2	2	3	2	2	3	3	2	2	2	3	3	3	2	2	4	2	2	-	-	-	47
2	1	1	0	1	2	2	3	1	2	3	3	1	2	3	3	3	2	1	-	-	-	-	34
3	0	0	0	0	2	1	2	2	2	3	3	3	3	1	2	3	2	1	-	-	-	-	30
4	1	0	1	1	1	1	2	2	2	2	3	2	3	2	2	3	2	4	3	2	-	-	39
5	1	1	1	2	2	2	0	2	1	3	2	2	2	1	2	1	2	3	2	3	1	2	38
6	2	1	1	2	1	3	1	2	2	3	2	2	1	3	2	2	2	-	-	-	-	-	32
7	1	1	0	1	0	1	1	1	1	2	3	2	2	2	3	1	2	3	2	3	-	-	32
8	0	0	1	2	1	1	0	2	2	1	3	3	2	2	1	4	2	6	-	-	-	-	33
9	3	1	2	2	2	3	3	2	2	1	4	1	2	2	5	0	2	1	-	-	-	-	38
10	1	0	1	0	4	2	2	2	2	2	3	2	2	2	3	2	3	1	2	-	-	-	37
Average																							36

It will be seen from these records that the general average per day was approximately 2, with a maximum of 6. In the laboratory, under forcing conditions in capsules as previously mentioned, as many as 8 eggs were obtained within a period of 6 hours, but this was abnormal and is not duplicated in the field.

TIPHIA VERNALIS Rohwer

GENERAL OBSERVATIONS

Tiphia vernalis is a Chosen species which has for its normal host *Popillia castanoptera*. It was found by the junior writer in May, 1922. In establishing the value of this and all other Chosen scoliids, they were first tested out on larvæ of *P. japonica* which were taken from Japan to Chosen for that purpose. If they readily accepted the Japanese Popillia, they were considered of economic importance and their study and rearing were continued.

In the studies of several species of Tiphia it was found that the group as a whole tends to be limited to a host genus rather than to a single species. *Tiphia vernalis* will accept grubs of *P. atrocoerulea*, but as a rule this host is physiologically unfit, being too near the pupal period to be readily parasitized. On the other hand, *P. japonica* is taken early enough to be suitable. In captivity this Tiphia has been reared on four species of Popillia.

FIG. 28.—Larva of *Popillia japonica* parasitized by *Tiphia vernalis*

In the spring of 1922 a few individuals were reared on *P. japonica* (fig. 28), but in 1923 this work was undertaken on a large scale with native hosts. Hundreds of females were collected in the field and brought to the laboratory for oviposition and rearing of larvæ. The same rearing methods were used as for the preceding species. At times as many as 450 females were on hand for this purpose. From a total of 5,785 eggs obtained at Suigen in 1923, 2,350 cocoons were obtained.

LIFE HISTORY AND HABITS

The adults of *Tiphia vernalis* are found in the field from May 5 to June 14, with a maximum abundance from May 19 to 25. Feeding takes place largely upon honeydew produced by aphides on pine, oak, and chestnut. The females are most abundant on chestnut foliage from 9.30 to 11.30 a. m. on warm, bright mornings. A low temperature tends markedly to slacken activity.

Although the adults seem to be very local in distribution, the parasitism of Popillia grubs in regions where the wasps were not abundant indicates that the species is more generally distributed than is evidenced by the presence of the adults alone.

Tiphia vernalis, although not of prime importance, is well worth introduction. Its occurrence in the spring is timely for Popillia in America, and if introduced with the preceding species would form the practical equivalent of a two-brooded species. On June 5, 1923, a count of 100 field-collected grubs gave a 10 per cent parasitism by *vernalis*.

The egg-laying habits of this species are similar to those of *Tiphia popilliavora*, except that the eggs are placed in the suture between the third thoracic and first abdominal segments on either side of the median ventral line (fig. 26), and with the anterior pole directed

toward the lateral margin. The time of oviposition is largely during the afternoon. The eggs are white or yellowish white, and 1 mm. in length. The duration of the stage is from eight to nine days. The hatching and feeding of the larvæ are similar in all respects to those of *T. popilliavora*.

The rate and duration of oviposition as determined for this species are indicated in Table 3. From this it will be noted that the species does not average 1 egg per day during the oviposition period, that the maximum number obtained in one day was 3, and that the average total per individual was 25. This is markedly lower than the records obtained for *Tiphia popilliavora*.

TABLE 3.—*Oviposition records of 10 females of Tiphia vernalis*

Female No.	May															
	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1	1	2	1	0	0	2	2	2	0	1	1	1	1	1	0	0
2	1	1	1	2	1	1	0	1	0	1	0	1	1	0	1	1
3	0	1	1	0	1	0	2	0	1	1	1	1	1	2	0	1
4	----	----	2	0	2	0	1	1	1	1	1	1	1	1	0	1
5	----	----	1	0	1	0	2	1	1	2	1	2	0	1	1	1
6	----	----	----	----	1	1	0	0	1	2	1	1	1	0	1	1
7	----	----	----	----	1	1	1	1	1	2	0	2	1	1	1	1
8	----	----	----	----	0	1	1	0	1	1	0	1	0	1	0	1
9	----	----	----	----	----	1	1	0	1	2	0	1	0	0	0	1
10	----	----	----	----	----	0	1	1	0	1	1	2	1	1	0	1

Female No.	June															Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
1	1	2	1	1	1	1	0	1	2	1	1	0	1	0	[1]D	----	28
2	2	1	0	1	1	1	1	1	2	1	1	0	0	1	D	----	26
3	1	0	1	1	0	1	1	0	1	2	2	2	0	0	D	----	25
4	2	1	2	0	1	2	0	1	2	1	1	0	1	1	D	----	28
5	2	1	0	0	1	2	0	1	1	2	1	2	1	0	0	D	28
6	2	1	0	1	0	0	1	2	1	1	2	0	[1]D	----	----	----	21
7	1	0	1	1	1	2	1	2	2	0	2	1	1	0	D	----	28
8	0	1	0	1	1	2	1	1	1	1	2	1	0	0	D	----	19
9	2	2	1	0	1	1	0	1	2	1	1	1	0	0	0	D	20
10	1	0	2	1	0	1	1	2	2	1	1	3	3	1	D	----	28
Average	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	----	25.1

[1] D indicates death of female.

The period of larval growth from the hatching of the egg to the spinning of the cocoon is 24 days, or slightly longer. In this species the period of growth is much more constant than in the Japanese species, a fact which is no doubt due to the increasing temperature of May and June in Chosen, whereas at Koiwai it decreases rapidly during August and September.

The cocoons are like those of the preceding species. Unlike those of most Tiphia, however, the larvæ transform to pupae in the fall and development advances to an almost perfect imago, in which state the winter is passed.

TIPHIA KOREANA Rohwer

GENERAL OBSERVATIONS

During the middle of August, 1923, there were found in a small locality near Suigen, Chosen, a few individuals of Tiphia which, when tested experimentally, oviposited readily upon grubs of *Popillia atrocoerulea* and *Anomala* sp. Later grubs of *P. japonica* were provided, and oviposition and development took place normally upon them. However, field collections of parasitized grubs indicated its true host to be Anomala rather than Popillia.

The adult wasps were very rare in the field at the time mentioned and only nine females were obtained. Examination on August 12 of field grubs bearing eggs or larvæ revealed practically all to be in the first larval stage, though a few eggs had not yet hatched. The proportion of Anomala grubs parasitized ranged as high as 76 per cent in small lots brought in by the collectors, the general average being 20 per cent for the area in which the parasite was known to occur. A consideration of the foregoing data would indicate that the period of adult presence ranged from about July 20 to the middle of August, with the peak of oviposition attained in the first week of the latter month, and that the few adults collected represented merely the end of the period rather than an actual numerical scarcity. A small number of cocoons were obtained from field-collected material and forwarded to the Riverton laboratory for rearing and liberation.

LIFE HISTORY

Unlike the other species of Tiphia discussed in this bulletin, *T. koreana* places its egg dorsally rather than ventrally upon the host, and in a crevice on the median line of the third thoracic segment. The egg is somewhat dark in color as compared with that of the two preceding species. Under relatively high temperature conditions hatching occurs in five to six days, but the larval stages in the field are prolonged as a result of the rapidly decreasing temperatures in the latter part of August and early September. The winter is passed in the larval stage within the cocoon.

The adults of this species are somewhat larger than those of *Tiphia popilliavora* and *T. vernalis;* in fact, they are the largest of all the species found in Chosen, and this combined with the earliness of their appearance would seem to handicap it considerably against *Popillia japonica* in America. With a largely biennial cycle of the host, as in Hokkaido, mature grubs would be available for parasitism during the period covered by this Tiphia, but very few such grubs are available in the American infestation. It is therefore seen that relatively little effectiveness can be looked for from its introduction.

KEY FOR THE DETERMINATION OF TIPHIA ADULTS

In order to facilitate the identification of the introduced species of Tiphia, S. A. Rohwer has prepared the following key. However, reference to further detailed description in his papers[5] is advisable. In this key the specific characters are inclosed in parentheses.

[5] Rohwer, S. A. Descriptions of three species of Tiphia parasitic on *Popillia japonica* (Hym.). *In* Proc. Ent. Soc. Wash., vol. 26, pp. 87–92, 1924. A new Tiphia from Korea (Hym.). *In* Proc. Ent. Soc. Wash., vol. 29, January, 1927.

1. Inner side of hind basitarsus without a longitudinal groove; propodeal enclosure distinctly narrowing posteriorly, about twice as long as greatest width, the median carina incomplete; about 12 mm. long; (anterior and dorsal margin of pronotum separated by a carina; side of pronotum without a groove; second intercubitus curved; punctures on tergites 3, 4, and 5 small, close, and evenly distributed) ..*koreana* Rohwer
Inner side of hind basitarsus with a longitudinal groove; propodeal enclosure nearly parallel-sided, the median carina strong, complete; about 10 mm. long 2
2. Anterior and dorsal margin of the pronotum separated by a carina; (legs black; basal part of pygidium striato-punctate, the apical part very minutely sculptured); Japan ..*popilliavora* Rohwer
Anterior and dorsal margin of the pronotum not separated by a carina; (second intercubitus distinctly curved; produced median portion of clypeus slightly emarginate apically); Japan and Chosen ..*vernalis* Rohwer

CRASPEDONOTUS TIBIALIS Schaum [6]

COLLECTION AND SHIPMENT

The carabid *Craspedonotus tibialis* (fig. 29) occurs abundantly in the sandy areas near Miho, a small seacoast village about 50 miles south of Yokohama. It is predacious in both the larval and adult stages, feeding upon a number of insect species, including the Scarabaeidae. Because of this habit it was thought worth while to introduce the species for experimental and study purposes at the Japanese Beetle Laboratory at Riverton, N. J. Consequently, in June and September, 1920, some 1,100 adults were forwarded, and these were followed by shipments of 15,350 beetles in June, 1921.

The beetles were collected by the women and children of the district (fig. 30, A), who became very proficient in locating them. Individual beetles were packed in small wooden safety-match boxes containing damp sphagnum moss. The match boxes were further packed in strong wooden containers which were roped together in sets of six (fig. 30, B).

Shipments were made in cool vegetable storage from Yokohama, but on arrival in the United States they crossed the continent at ordinary temperatures. These shipments reached the laboratory at Riverton with a mortality of approximately 50 per cent. Since a considerable mortality had been anticipated allowance was made for this by shipping unusually large numbers.

LIFE HISTORY AND HABITS

There is one generation annually, and hibernation takes place apparently in the last larval stage. Adults appear in abundance at Miho in June. In the collections made from June 1 to 6 many of the beetles were not completely hardened, indicating that they had very recently changed from the pupal stage.

The adults live in deep tubular burrows 10 to 18 inches in depth and enter the soil at an angle of about 45°. The time spent in these burrows by the female beetle must be considerable, extending through the mating and egg-laying periods. Often at the lower end of the burrow the remains of scarabaeid beetles were found.

The eggs are laid in small cells or chambers one-half inch deep, which angle off in a downward direction from the sides of the main

[6] The first observations upon the habits of *Craspedonotus tibialis* were made by Frederick Muir, of the Hawaiian Sugar Planters' Experiment Station, and it was through the entomologists of that station that information was obtained regarding the localities in which it could be found in abundance.

burrow. The entrances to the egg cells are filled with sand so as to close them off from the burrow inhabited by the female. As many as 9 to 11 cells are formed, each containing a single egg.

All attempts to establish this species were unsuccessful, these failures probably being due to a decided change in the ecological habitat. In Japan Craspedonotus is found only in sandy regions with open vegetation, whereas at Riverton the place of introduction was a heavier soil covered with a dense plant growth. Since this beetle is found in the sandy banks at Koiwai in northern Japan, it would seem that the temperature factor was not the limiting one in the failure of the species to become established in America.

FIG. 29.—*Craspedonotus tibialis*, female

LIFE HISTORY OF POPILLIA JAPONICA IN JAPAN

As has been previously mentioned, the varying life cycle of Popillia as it occurs in Japan has an important bearing on certain of its parasites. When this is compared with the life cycle in the United States it will be seen that further conditions will undoubtedly arise which will have an important bearing on the parasite-introduction problem, and it is therefore important that these points should be further discussed.

Popillia japonica is found on all of the main islands of Japan, but does not extend to the Asiatic mainland. It is most abundant in the northern half of Honshu and all of Hokkaido in the areas where grasslands occur. This northern habitat corresponds somewhat in climate to that of New Jersey and Pennsylvania. Nowhere in Japan is it a pest of much economic importance.

At Yokohama (lat. 35.5° N.) Popillia is common but not abundant enough to be of any importance as a plant pest. Here the first beetles of the season appear as early as May 28, the maximum numbers being found in the field about June 20, after which date a gradual decline takes place and by July 25 only a very few stragglers are found.

In this locality one complete generation occurs each year, there being no evidence of larvæ going over a second season; in fact, all reach the third instar by mid-September of the year in which the eggs are laid.

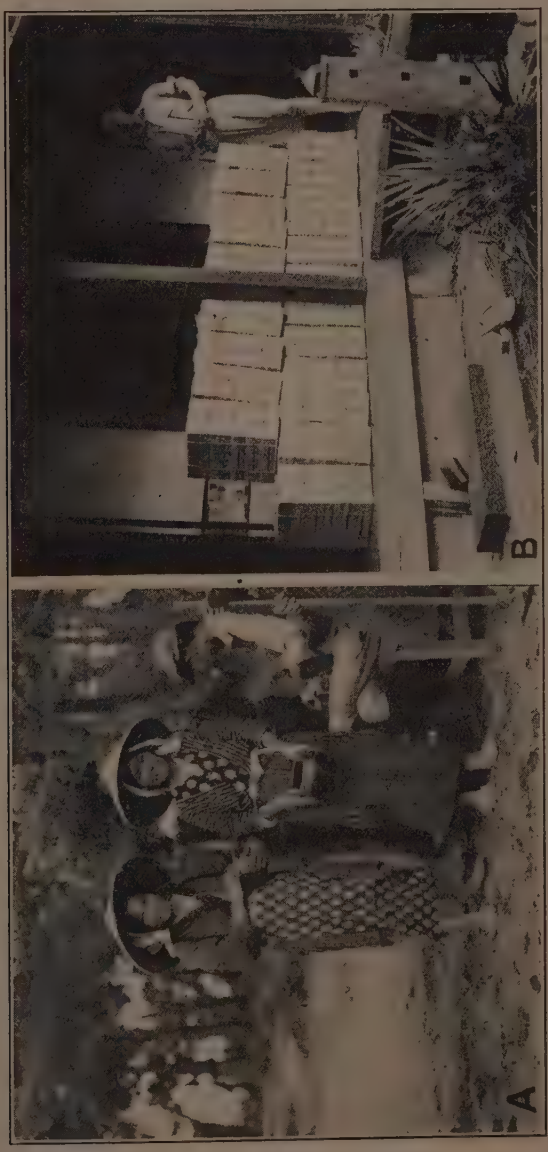

FIG. 30.—A, collectors of *Craspedonotus tibialis* at Miho, Japan; B, 10,000 beetles of *C. tibialis* packed for shipment to the United States from Miho, Japan

At Koiwai (lat. 39.5° N., altitude 1,500 feet), a small village about 10 miles from Morioka and 300 miles north of Yokohama, the

climate is considerably colder than at the latter place, the growing season being confined to June, July, and August. Because of the grass and meadow lands here Popillia is more abundant than southward, although it is not an economic pest. The first beetles of the season appear about July 1, increasing rapidly to maximum numbers by July 24, after which the decline is gradual through August, and by September 10 only a few are left. Here approximately 25 to 30 per cent of the beetles undergo a two-year cycle. This condition seems constant in northern Honshu.

At Sapporo (lat. 43° N.), on the island of Hokkaido, and about 520 miles north of Yokohama, Popillia is more abundant than elsewhere in Japan, perhaps because of the presence of extensive grass and meadow lands which afford undisturbed breeding grounds. It is said that at times the adults occur in such numbers as to cause damage to the foliage of the soybean, although in four years' observations by the writers no material damage to any economic crop was noted.

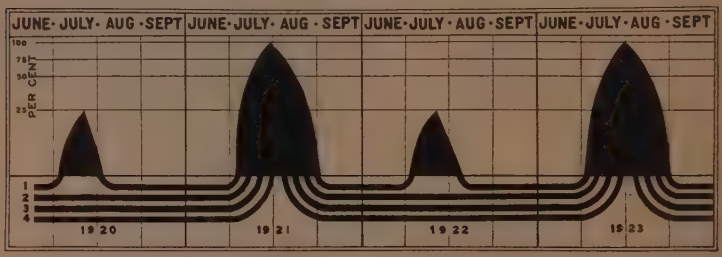

FIG. 31.—Diagrammatic calendar of the fluctuating biennial broods of *Popillia japonica* at Sapporo, Japan. Lines 1, 2, 3, and 4 represent, respectively, 25 per cent of the stages passed in the soil, eggs, larvæ, and pupæ. Solid black curves represent adults as they occur during the seasons. Winter months are omitted for convenience. The years 1920 and 1922 were seasons in which only 25 per cent of the larvæ (No. 1) transformed to adults, larvæ Nos. 2, 3, and 4, or 75 per cent, remaining in the soil to transform the following seasons. The years 1921 and 1923 were seasons in which practically all larvæ transformed into adults. Curves for adults in 1920 and 1922 have their apices about July 20, or 10 days earlier than normal, because of the intensive parasitism by *Centeter cinerea*. Curves for adults in 1921 and 1923 represent normal abundance with apices at the end of July, *C. cinerea* not being abundant enough to affect the decline as in the preceding years. This fluctuating condition seems to be constant for this region

In this region Popillia has largely a two-year life cycle with about 75 per cent of the adults emerging in alternate years (see fig. 31). Thus 1920 and 1922 were years of minimum emergence, comprising about 25 per cent of the beetle fauna. During these years the first adults appeared about July 5, the maximum numbers occurring about July 22, followed by a rapid decline and the disappearance of the beetles by the first week in August. This latter condition is due to the parasitism of the adults by *Centeter cinerea* and is discussed under that head. In the years of greatest abundance (1921 and 1923) the first beetles appeared about July 5 also, and reached the maximum by the end of the month. The decline was gradual through August and by early September all had disappeared.

In the years of adult abundance virtually all larvæ develop into adults, only a fraction of 1 per cent of the total number remaining in the larval stage by the end of July. These doubtless comprise two-year cycle grubs which originated from the 25 per cent of one-year beetles. It is also presumed that a fraction of the progeny of the two-year beetles may revert to the one-year cycle. During the

periods of larval scarcity it is impossible to obtain sufficient numbers for experimental purposes.

As contrasted with the life cycle of Popillia at Sapporo and Koiwai, Japan, that in the United States in the infested area of New Jersey is as far as known entirely of one year, corresponding in this respect to the condition existing at Yokohama. At Riverton the first beetles issue in numbers in mid-June, and the maximum emergence is reached from July 10 to 20. From the end of July or mid-August, according to the season, the decline in numbers takes place, coming to a close in mid-September.

FOOD PLANTS OF POPILLIA IN JAPAN

During four years' study of Popillia in Japan, the writers have not observed it as a serious pest, although Japanese entomologists have recorded it as at times doing considerable damage to soybean plants. As regards this particular food plant, we may cite the condition existing during the summer of 1921 at Koiwai, where feeding by the beetle was largely upon *Polygonum reynoutria* growing along the roadside bordering the breeding grounds, and immediately adjoining it was a large field of soybeans. Although the Polygonum foliage was almost skeletonized, hardly a single individual was found in the adjoining soybean field. At Koiwai also, where considerable corn is grown, there is no damage to the silks or to green corn. However, at Riverton corn silk and green corn are favorite foods. Likewise wistaria at Yokohama is much fed upon by Popillia, yet wistaria at Sapporo is rarely touched. These points illustrate a common feeding habit, namely, that the favorite food plants of one district, although present in another, are often not fed upon by the beetles.

The favorite food plants in the three localities in which observations were most extensive are listed in Table 4.

TABLE 4.—*Favorite food plants of Popillia japonica at Tokyo, Koiwai, and Sapporo*

Locality and botanical name	Common name	Parts of plant eaten
Tokyo, Yokohama region:		
Cissus japonica	Blind grape	Leaf and flowers.
Wistaria floribunda	Wistaria	Leaf.
Vitis sp	Cultivated grape	Leaf and flowers.
Castanea sp	Chestnut	Flowers.
Koiwai:		
Polygonum reynoutria	Itadori	Leaf and flowers.
Rumex sp	Dock	Do.
Populus nigra	Italian poplar	Do.
Pteridium aqualinum	Fern	Do.
Sapporo:		
Polygonum reynoutria	Itadori	Do.
Prunus japonica	Hedge plum	Leaf.
Populus nigra	Italian poplar	Do.
Vitis sp	Cultivated and wild grapes	Leaf and flowers.

Table 5 gives a more complete list of the food plants of *Popillia japonica*. The list includes a few foreign plants commonly grown in Japan.

TABLE 5.—*Food plants of Popillia japonica in Japan*

FOR THE REGION OF TOKYO, YOKOHAMA, AND SOUTHWARD

Botanical name	Common name	Parts of plants eaten
Trees:		
Castanea pubinervis [1]	Chestnut	Leaf and flowers.
Quercus variabilis	Oak	Leaf.
Quercus serrata	do	Do.
Populus maximowiczii	Poplar	Do.
Populus nigra [1]	Italian poplar	Do.
Ulmus parvifolia	Elm	Do.
Zelkova serrata	Kiaki	Do.
Tilia japonica	Linden	Do.
Tilia mequeliana	do	Do.
Alnus japonica	Alder	Do.
Prunus serrulata	Cherry	Do.
Melia japonica [1]	Sendan	Flowers.
Shrubs:		
Rosa multiflora	Rose	Leaf and flowers.
Hibiscus syriacus	Hedge plant, nonindigenous	Leaf.
Dioscorea japonica	Yumanorma	Do.
Vines:		
Vitis thunbergii [1]	Wild grape	Leaf and flowers.
Vitis vinifera [1]	Cultivated grape	Do.
Cissus japonica [1]	Blind grape	Do.
Wisteria floribunda [1]	Wistaria	Leaf.
Smilax china	Smilax	Do.
Herbaceous plants:		
Glycine soja	Soybean	Leaf and flowers.
Phaseolus vulgaris	Common bean	Do.
Polygonum convolvulus	Sendanoki	Do.
Polygonum reynoutria [1]	Itadori	Do.
Polygonum thunbergii	Mizosoba	Do.
Polygonum nodosum	Oinutade	Do.
Asparagus officinalis	Asparagus	Do.
Rumex sp.	Dock	Leaf.

FOR REGION NORTH OF TOKYO TO SAPPORO

Trees:		
Castanea pubinervis [1]	Chestnut	Leaf and flowers.
Populus nigra [1]	Italian poplar	Leaf.
Zelkova serrata	Kiaki	Do.
Prunus japonica	Hedge plum	Do.
Platanus orientalis	Sycamore	Do.
Filipendula kamtchatica	Filipendula	Do.
Berchemia racemosa	Kumayanagi	Do.
Salix purpurea	Willow	Do.
Shrubs and vines:		
Rosa spp.	Wild roses	Leaf and flowers.
Vitis spp [1]	Cultivated and wild grapes	Do.
Rubus crataegifolius [1]	Kumaichigo	Leaf.
Herbaceous plants:		
Polygonum reynoutria [1]	Itadori	Leaf and flowers.
Oenothera biennis	Primrose	Do.
Glycine soja	Soybean	Do.
Asparagus officinalis [1]	Asparagus	Do.
Pteridium aqualinum [1]	Fern	Leaf.
Hypericum sp.	St. John's wort	Flowers.
Trifolium pratense	Red clover	Do.
Rumex sp.	Dock	Leaf.

[1] Favorite food plant.

CLIMATIC CONDITIONS IN THE MAIN FIELDS OF INVESTIGATION

A comparison of the climatic conditions in the various regions in which work was conducted with those in the infested area in America is of value from two points of view: (1) In relation to the reactions of *Popillia japonica* itself under varying conditions, and (2) as bearing upon the question of establishment of the oriental parasites in this country.

Figure 32 gives a graphic representation of the mean monthly temperatures throughout the year for Yokohama, Koiwai, and

Sapporo, Japan, and Suigen, Chosen, the four main centers of investigation. These graphs show a considerable uniformity in certain respects, the peak in each case occurring in August and followed by a sharp decline. Sapporo is uniformly 6 to 10° C. (11 to 18° F.) cooler than Yokohama, with Koiwai occupying an intermediate position. In Chosen, on the contrary, the summer temperatures approximate those at Yokohama, whereas during the winter they coincide closely with those of Koiwai and Sapporo.

A comparison of these records with the graph shown in Figure 33, which is for Philadelphia, brings out several interesting points. The winter temperatures at the latter place are 4 to 6° C. (7 to 11° F.) above those of Koiwai, Sapporo, and Suigen, whereas the graph for

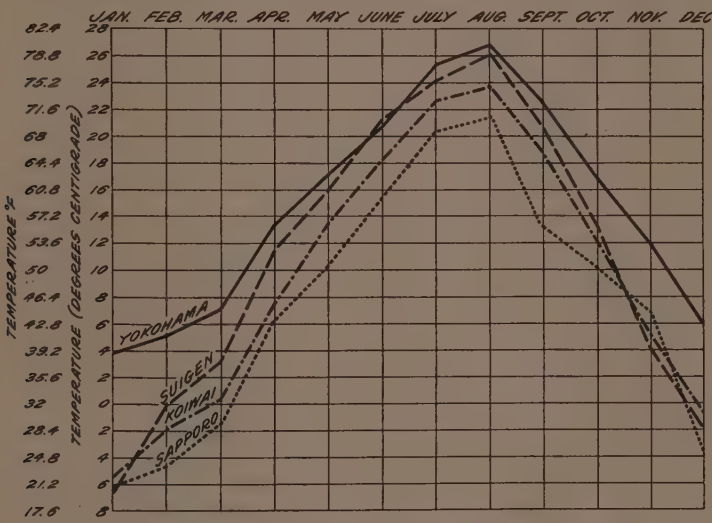
JAN. FEB. MAR. APR. MAY JUNE JULY AUG. SEPT. OCT. NOV. DEC.
82.4 78.8 75.2 71.6 68 64.4 60.8 57.2 53.6 50 46.4 42.8 39.2 35.6 32 28.4 24.8 21.2 17.6
28 26 24 22 20 18 16 14 12 10 8 6 4 2 0 2 4 6 8
TEMPERATURE °F.
TEMPERATURE (DEGREES CENTIGRADE)
YOKOHAMA
SUIGEN
KOIWAI
SAPPORO

FIG. 32.—Curves showing the range of the mean monthly temperature for Yokohama, Koiwai, and Sapporo, Japan, and Suigen, Chosen. Temperature based on a three-year average, except Yokohama, which is for two years

the spring months follows very closely that of the latter place. The maximum summer temperature is attained in July rather than August, and the decline which follows is more gradual. Thus it is seen that the growing season at Philadelphia is nearly six weeks longer than at Koiwai or at Sapporo, and this in a measure explains the more or less biennial cycle of *Popillia japonica* in northern Japan as contrasted with the normal one-year cycle at Yokohama and in America.

Figure 34 shows the mean monthly precipitation for Yokohama, Sapporo, and Suigen, based on a two-year average, and Figure 33 shows that for Philadelphia on a 50-year average. Unfortunately it was not possible to obtain records for Koiwai, and although those for Morioka, 10 miles away, were available yet these were in no wise comparable to the Koiwai figures. A heavy snowfall occurs in the winter months and fairly heavy rains are not infrequent throughout the remaining portions of the year, in fact daily showers are a rather notable feature.

It is seen by reference to Figure 34 that rainfall at Yokohama was very light in the winter but fairly heavy in the summer months, whereas at Sapporo the heaviest precipitation was recorded in the winter, with the lowest points reached in the early summer months.

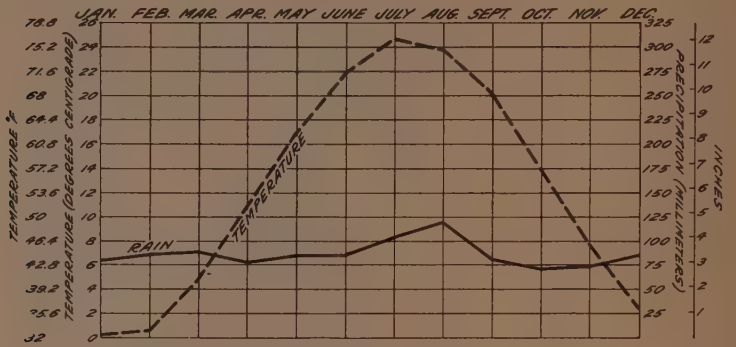

FIG. 33.—Curves showing the mean monthly temperature and precipitation for Philadelphia, based on a 50-year average

At Suigen, Chosen, however, the winter and spring precipitation is very low, followed by a period of exceedingly heavy rainfall during July and August. The rainfall during the 24 hours of July 28, 1922 totaled 11.3 inches. A comparison of these graphs with that of

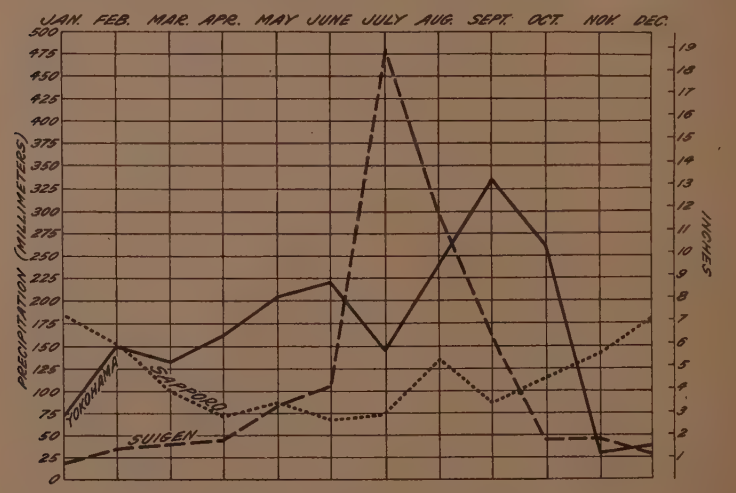

FIG. 34.—Curves showing the mean monthly precipitation for Sapporo and Yokohama, Japan, and Suigen, Chosen, based on a two-year average

Philadelphia shows that Sapporo, and probably Koiwai as well, correspond fairly closely, whereas the heavy summer and light winter precipitation at Yokohama and Suigen are far removed from it.

A consideration of the two factors of temperature and rainfall in the various localities reveals the fact that conditions at Koiwai and

Sapporo more nearly approximate those of the infested area than do those at Yokohama and at Suigen.

AGRICULTURE AND NATURAL LANDS OF JAPAN AND CHOSEN IN RELATION TO POPILLIA

Since agricultural and natural conditions have an important bearing upon the fauna, it is relevant here to make a few remarks concerning them.

The combined area of the main islands—Honshu, Kyushu, Shikoku, and Hokkaido—is 140,000 square miles, or approximately the same as the area of Montana. A large part of this area consists of mountainous country heavily forested with virgin and planted forests. Much of the land is worthless "hara," or rolling prairielike lands at the foot of the higher mountain ranges. These are densely covered with low, persistent bamboo grasses. Sand hills and plains along the coast also form a distinct habitat of considerable extent. About 17 per cent of the total land area is estimated as arable, although only 12 per cent is under actual cultivation.

The limited area of arable land and the food supply demands of this densely populated country have made Japanese agriculture one of the most intensive in the world (fig. 35). Rice is the chief food and it is grown largely in flooded plots called "paddy fields," one-half of the agricultural lands being given over to this crop. The average landholding in this agricultural area is 2½ acres per individual. Where physiographical conditions were originally unfavorable, they have been altered if possible to suit rice growing. This has resulted in the terracing of hill and mountain sides and the cutting up of the lowlands into innumerable paddy fields to accommodate them to the varying water levels. Where it is possible to drain the paddy fields they are immediately prepared for wheat or barley as a successive crop. Areas not suited to rice culture are devoted to dry farming, including the growth of wheat, barley, rye, millet, soybeans, nd such vegetables as daikon radishes, eggplants, sweet potatoes, taro (*Caladium colocasia*), and Japanese onions (negi). All these food plants, including such grains as wheat and rye, are cultivated and fertilized intensively during their growing period, and often eggplants, onions, or cucumbers are grown betweeen the rows of grain.

On the island of Hokkaido, natural and agricultural conditions more nearly approach those of our Eastern States. There are large areas of natural forest similar in makeup to our own forests, the trees consisting of species of oak, maple, beech, magnolia, chestnut, birch, and pine. The extent of waste lands in Hokkaido compares with that of Pennsylvania. Agricultural landholdings in this region are somewhat larger than in Honshu and the method of cropping is similar to that in America. Corn, wheat, oats, barley, rye, millet, and some rice are the chief grains grown. Grasslands suitable for grazing are more abundant here than elsewhere in Japan, and dairying and stock farming are resulting industries.

Koiwai, near Morioka on the island of Honshu, is not in the zone of intense agriculture, but is in reality one large estate of 7,500 acres in an old volcanic upland of sufficient elevation for the development of natural grasslands and grains, such as corn, wheat, and oats, and the methods of cropping are like those employed in the eastern

section of the United States. The forest areas here are entirely artificial, consisting for the most part of regular plantings of chestnut, larch, and pine.

These agricultural conditions may be a factor influencing the relative abundance of *Popillia japonica* within certain regions. From Sendai southward is the region of intense cultivation, as

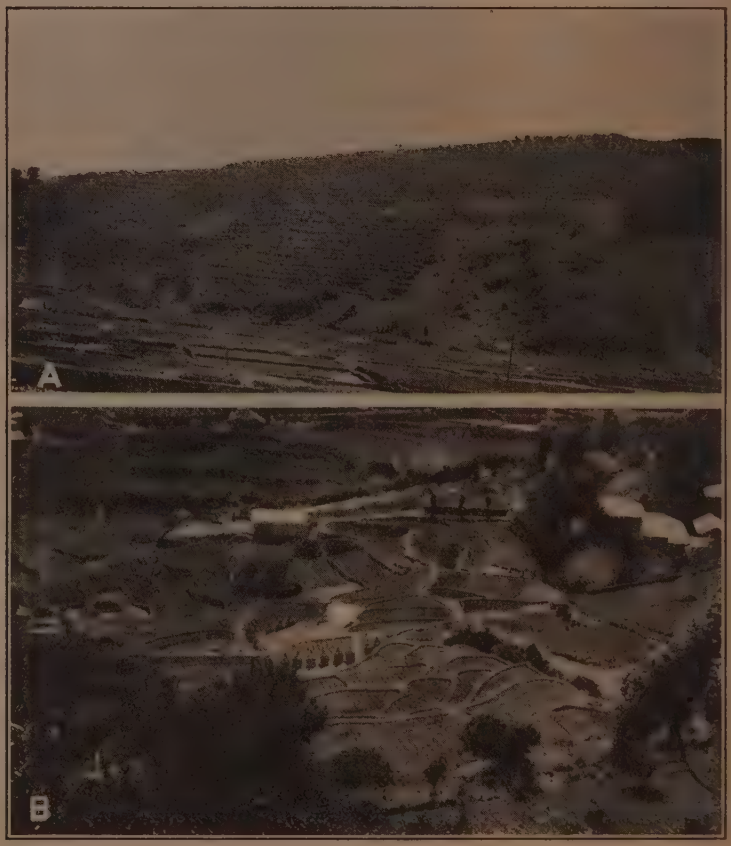

FIG. 35.—A, terraced hillside planted with orange trees, showing intensive agricultural conditions in southern half of Japan; B, rice paddy lands in a valley, illustrating intensive agricultural conditions in central Japan

described in the preceding paragraphs, and within this region Popillia is much less abundant than northward. This lack of abundance may be the result of the intense cropping of the soil and the flooding of the paddy fields, practices which are most unfavorable for soil-inhabiting insects. Further, within this region there are very few grasslands other than dense growths of low bamboo grass, these latter being rarely inhabited by Popillia. On the other hand, north of Sendai, including Koiwai and the island of Hokkaido, Popillia is

more abundant than elsewhere in Japan. Here agriculture is not so intensive, waste lands are more extensive, and sod or pasture lands in which Popillia breeds are not uncommon. Food plants suitable for the adults, however, are no more abundant here than in the south.

The foregoing points have been considered for the reason that they are thought by some to be the chief factors influencing the distribution of Popillia; but the writers are of the opinion that this insect is more abundant in the north because it is by nature a species which has become adapted to a northern habitat. At Tokyo and Yokohama, where sod lands have been artificially produced in lawns and golf links, Popillia does not increase and take advantage of these breeding grounds.

In Chosen agricultural conditions, although similar to those of Japan, are not so intensive. The outstanding feature in that country is the lack of forests. As a result of this forest destruction vast mountain areas have lost their soil and support no vegetation. In the lowlands grasses grow in all the waste places and in these areas the Chosen species of Popillia are commonly found.

THE SPECIES OF POPILLIA IN CHOSEN

Of the five or six species of this genus said to occur in Chosen only three are common and widely distributed.

POPILLIA ATROCOERULEA Bates

During the season the first species of Popillia to appear is *P. atrocoerulea*. This is a large species measuring from 11 to 13 mm. in length. It is entirely dark blue and has lateral tufts of white hairs on the abdominal segments. A common variety of this same species has the basal half of the elytra marked in deep chestnut brown.

The first beetles appear about the first of June and all disappear by the end of the month. They are most abundant about the time of full bloom of the Chosen chestnut during mid-June.

Only a few individuals have been reared through their life cycle. Egg laying is largely in grasslands, and the duration of the stage averages 12 days. There are three larval instars, the winter being passed in the third stage.

The chief food plants of this species are the flowers of the Chosen chestnut (*Castanea crenata*), leaves of the goumi bush (*Elaeagnus umbellata*), and the leaves of both wild and cultivated grape, the nonpubescent races being more readily eaten. These beetles have a strong tendency to feed on flowers, and are very destructive to roses.

POPILLIA CASTANOPTERA Hope

This species is second in seasonal occurrence. It is a small beetle 8 to 10 mm. in length, with the thorax bright metallic green and the elytra bright chestnut brown.

This is an abundant species and is found from late June to mid-August. The larvæ inhabit sod lands. Hibernation takes place in the third and final instar.

The important food plants of the adult are red straw (*Galium verum*), both leaves and flowers, leaves of *Quercus serrata*, a number of species of smartweed (*Polygonum* spp.), leaves and flowers of chestnut (*Castanea serrata*), leaves of goumi (*Elaeagnus umbellata*), and wild and cultivated grapes.

POPILLIA MUTANS Newm.

This third Chosen Popillia is much less abundant than the preceding two. The adults are robust beetles from 11 to 13 mm. in length, entirely deep indigo blue in color, and resembling somewhat the blue forms of *P. atrocoerulea*, but distinguishable from them by the absence of the abdominal tufts of white hair.

This is a late-appearing species, being found from mid-August to mid-September, and at no time is it abundant. Larvæ are found feeding on the roots of grasses. Only a few individuals have been reared through the life cycle, and these hibernated in the second larval instar.

The adults are flower feeders, confining their attention almost exclusively to the flowers of bush clover (*Lespedeza bicolor*), though they occasionally feed on flowers of other clovers.

SUMMARY

Nine species of parasites and one predator of the Japanese beetle (*Popillia japonica*) have been found and studied in Japan and Chosen. These represent three species of tachinids, two dexiids, four scoliids, and one carabid.

Among the tachinids *Centeter cinerea* is the most promising species, for in its native habitat it is very abundant and exerts a marked control upon *Popillia japonica*. In Hokkaido the largely two-year life cycle of the host interferes with its rate of increase, so that in successive years the percentage of parasitism fluctuates from approximately 20 to 90, respectively. At Koiwai in northern Honshu, where the number of beetles is fairly constant each year, the parasitism averages somewhat above 50 per cent. The climatic conditions under which this species lives correspond fairly closely to those of the infested locality in America.

Ochromeigenia ormioides is more common in the warmer regions of Japan, though it ranges into Chosen and northern China, which would indicate that it is not limited to mild climatic conditions. This parasite is extremely sporadic in its attacks upon *P. japonica*. In some seasons parasitism reaches 35 per cent in a given locality, but in the following seasons it may fall below 2 per cent. A secondary host is necessary for the overwintering brood. The establishment of the species therefore depends upon its ability to become adapted to a new alternate host in America, if such is available.

Eutrixopsis javana has been obtained only from Hokkaido, and in that locality is of very minor importance as compared with *C. cinerea*.

Of the Dexiidae two species have been found to parasitize Popillia larvæ. *Prosena siberita* occurs abundantly in northern Japan and *Dexia ventralis* in Chosen. Living larvæ are deposited on the soil and these burrow about in search of host grubs, into which they penetrate and upon which they feed. *P. siberita* has but a single brood each year and is well adapted to its host as regards the time of appearance. It effects a field parasitism in Japan of approximately 10 per cent. *D. ventralis* has three broods per year and apparently requires a different host for each one. The establishment of this parasite in America depends upon the presence of additional hosts which pupate at a time favorable to the brood of Dexia.

Its rate of increase will also depend upon the numerical abundance of these hosts, if such are available.

Four species of Scoliidae have been found which either normally attack *Popillia japonica* or readily accept it as a host. *Campsomeris annulata* readily accepts full-grown grubs of *P. japonica*, but success in establishing it will depend upon the abundance of other acceptable native grubs which will support the broods for which large Popillia grubs are not available.

Of the Tiphia species, *T. popilliavora* at Koiwai effects a parasitism of 20 per cent upon grubs of *P. japonica*. It is a fall species, occurring during late August and early September. *T. vernalis* is a spring species occurring in Chosen during May and early June. It effects a field parasitism of 10 per cent upon native Popillia, and it readily accepts *P. japonica*. *Tiphia koreana* from Chosen is normally parasitic upon *Anomala* sp., but readily accepts *P. japonica*. The average parasitism by this species in the field is 20 per cent, but ranges at times as high as 76 per cent.

Craspedonotus tibialis is the only predator which has been considered for introduction. Large numbers were forwarded, but establishment was not successful.

In the Orient *Popillia japonica* is found only in Japan proper, and in that country it is of very minor importance as an enemy of economic crops. The most striking difference in its life history in Japan is the occurrence of a two-year cycle in 75 per cent of the total Popillia fauna on the island of Hokkaido. At Koiwai, in northern Honshu, only 25 to 30 per cent undergo a two-year cycle, whereas for Yokohama and regions southward only a one-year cycle is found.

Three species of Popillia occur commonly in Chosen, aud the chief importance of these lies in the fact that their special parasites may be of use in combating *P. japonica* in America. The known parasites of these have been tested on the latter host, and in all cases have accepted it readily.

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